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THE PUFFERFISHES (TETRAODONTIDAE) OF THE ATLANTIC OCEAN

by
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C. E. Dawson, Ed.

THE PUFFERFISHES (TETRAODONTIDAE) OF THE ATLANTIC OCEAN[1]

Robert L. Shipp

Pufferfishes are highly specialized representatives of the osteichthyean order Tetraodontiformes (=Plectognathi). All are capable of inflation by taking water or, less normally, air into an anterior evagination of the stomach. The absence of the pelvic girdle and various other osteological modifications are associated with the ability to inflate (Rosen, 1916). Most are tropical shore species, but some are from temperate regions, while a few frequent depths of more than a thousand meters. All warm seas have numerous endemic forms, but a few species are circumglobal. About eight puffers from Africa and Asia and at least one from South America occur primarily in fresh water.

In some areas, especially the western Pacific, pufferfishes are commercially valuable and highly regarded as food fish. More than four million pounds of the northern puffer, *Sphoeroides maculatus,* valued at more than $152,000, was landed in the Chesapeake Bay region in 1969 (National Marine Fisheries Service, 1969). However, many tropical species are capable of producing a powerful poison, tetrodotoxin, which has a potentially lethal inhibitory action on nerve impulse transmission, and elaborate precautions should be undertaken when pufferfishes are cleaned and prepared for consumption. Research on the toxin has been active during the last seventy-five years, and excellent summaries of the field are available from Mosher et al. (1964), Russell (1965 and 1969), Fuhrman (1967), and Halstead (1967).

[1]Most of the information contained herein was submitted to the Faculty of The Florida State University in partial fulfillment for the degree of Doctor of Philosophy.

The systematics of these fishes received little attention during this century. Nineteenth century attempts to clarify evolutionary relationships were hampered by lack of adequate study materials, as well as by misconceptions regarding the systematic importance of various anatomical structures (Regan, 1902:284; Fraser-Brunner, 1943:1). Contemporary nomenclatural difficulties result from an abundance of inadequate eighteenth and nineteenth century descriptions which were all to frequently based on earlier inadequate descriptions.

This situation has resulted in a systematic hodgepodge which has hampered investigators concerned with any phase of the biology of pufferfishes. For example, findings concerned with range extensions, species distribution, faunal relationships between different geographical regions, and species-specificity of tetrodotoxin, have sometimes been partially or wholly erroneous due to inadequate systematic knowledge of these fishes.

This research purports to resolve the systematics of those species of pufferfishes (family Tetraodontidae) which inhabit the Atlantic Ocean and adjacent marine and estuarine waters. Due to the large number of specimens examined in a study of this nature, significant data concerning various aspects of the biology of pufferfishes have been obtained for a large number of species and are included herein. A special effort has been made to correlate zoogeographic patterns with morphological similarities, and thus to interpret the evolutionary history of the group.

Seventeen species representing four genera of the family are recognized from Atlantic waters. Twelve species belonging to two genera (*Colomesus asellus, C. psittacus, Sphoeroides dorsalis, S. georgemilleri, S. maculatus, S. nephelus, S. parvus, S. spengleri, S. testudineus, S. tyleri, S. yergeri*) are restricted to the western Atlantic. Two species in two genera (*Ephippion guttifer, Sphoeroides marmoratus*) occur exclusively in the eastern Atlantic. The remaining three species, two of the genus *Lagocephalus,* (*L. laevigatus, L. lagocephalus*) and *Sphoeroides pachygaster* are trans-Atlantic, and possibly circumblobal (Table 1).

METHODS

Measurements and counts are as defined by Hubbs and Lagler (1958: 19-28) unless otherwise stated. Measurements were made with dial calipers, or dividers and millimeter rule. Measurements greater than 100 mm were made to the nearest 1.0 mm; measurements less than 100 mm were taken to the nearest 0.1 mm. All measurements and color descriptions are from preserved specimens.

Head length was measured from the anteriormost edge of the gill opening to the anterior premaxillary margin.

The ventrolateral body angle is defined as the sharp, nearly perpendicular angle formed at the junction of the lateral and ventral body surfaces.

Dorsal and anal fin ray counts include all visible rays, branched and unbranched. The last two rays, commonly counted as one in most systematic groups, are counted separately because they have separate bases. Pectoral fin ray counts exclude the dorsalmost rudimentary ray because it may not be visible or produced in some species. Fin lengths were determined by measurement of the exposed length of the longest ray, rather than measurement from its actual embedded base. Caudal length was determined by measurement of the exposed length of the medial caudal rays.

Descriptions of lateral line patterns and general osteology are included under discussions of genera only, as intrageneric variation of these characters is usually minor.

Proportional measurements of various regions (e.g., snout (length) in head, dorsal (fin length) in snout) which facilitate identification are included in the description of each species. Tables of the measurements as a percentage of standard length are also provided. These tables are based on 20 adult (sometimes large subadult) specimens in good state of preservation chosen randomly from throughout the geographic range of the species. Where 20 specimens were not available, all suitable material was used to compute these tables. Occasionally a specimen was partially damaged and was therefore excluded from certain measurements.

Repositories of specimens examined are: Academy of Natural Sciences of Philadelphia (ANSP); British Museum of Natural History (BMNH); Estacion de Investigaciones Marinas de Margarita, Venezuela (EIMM); Field Natural History Museum, Chicago (FNHM); Fisheries Research Board of Canada (FRBC); Florida State Board of Conservation, now the Department of Natural Resources (FSBC); Florida State University (FSU); Gulf Coast Research Laboratory Museum (GCRL); Institute of Marine Science, University of Texas (IMST); Jacksonville University (JU); Los Angeles County Museum (LACM); Louisiana Cooperative Fisheries Unit (LCFU); Musee Royal do l'Afrique Centrale, Tervuren, Belgium (MRAC); Museo Argentino de Ciencias Naturales, "Bernardino Rivadavia", Buenos Aires, Argentina (MACN); Museu de Zoologia da Universidade de Sao Paulo, Brazil (MZUSP); Museum National d'Histoire Naturelle, Paris (MNHN); National Marine Fisheries Service, Galveston, Texas (NMFS-G); National Museum of Natural History, Smithsonian Institution (USNM); Rijksmuseum van Natuurlijke Histoire, Leiden (RMNH); Stanford University, now at California Academy of Sciences (CAS-SU); Tropical Atlantic Biological Laboratory (TABL), specimens to be incorporated into the University of Florida (UF) collection; Tulane University (TU); University of Alabama (UAIC); University of Costa Rica (UCR); University of Florida (UF); University of Georgia (UG); University of Miami, Rosenstiel School of Marine and Atmospheric Sciences (UMML); University of North Carolina, Wilmington (UNCW); University of Puerto Rico (UPR).

The number of specimens examined with size range in standard length

is given in parentheses following the catalogue number for each series. More detailed collection data of series examined are included in Shipp (1970).

Synonymies include all known original usages of taxonomic names, as well as all references of systematic and zoogeographic importance. Simple check lists have been included when these were located with reasonable effort through interlibrary loan services, or by personal search at a number of large libraries. References of systematic importance which omitted species descriptions or figures in their discussion, or in which specimens are cited that have not been personally examined and which were collected from areas that cast doubt on their proper identification, are preceded by a question mark (?). Pre-Linnaean literature is not included in the synonymies, but is cited in the text where appropriate. Although synonymies are not extensively annotated, enough information accompanies each reference to identify its scope and area. When various spellings of a generic name are used, the rejected spellings are included in parentheses. Nomenclatural terminology is as defined in the International Code of Zoological Nomenclature (1964).

ACKNOWLEDGMENTS

I thank specifically those whose help was essential to the completion of this study. William I. Follett, California Academy of Sciences, liberally provided opinions and judgements on various nomenclatural dilemmas. Geoffrey Palmer, British Museum (Natural History), devoted two full days to assisting my literature search of rare books at that museum. Yseult Le Danois, Museum National d'Histoire Naturelle, Paris, fought the language barrier with me for nearly a week in Paris so that I could accomplish my goals there. Hugo Patricio Castello, Universidad del Salvador, San Miguel, Argentina, photographed and arranged shipment of Argentine material. Richard Bishop, Peace Corps volunteer, spent many hours in Nicaragua collecting and packing specimens for me. James C. Tyler, then at the Academy of Natural Sciences of Philadelphia, offered many days of assistance during my two visits to Philadelphia, and continually guided and advised my research from his background in plectognath systematics. James R. Martin, Cape Fear Technical Institute, donated his entire vacation in the summer of 1967 to assist in the collection of specimens. I give special gratitude to my major professor, Ralph W. Yerger, and to my wife Linda.

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HIERARCHAL SYSTEMATICS AND RESTRICTION OF FAMILIES

Pufferfishes have variously been considered as members either of many genera within a single family, Tetraodontidae, or of numerous families of which Tetraodontidae and the other families contain various numbers of genera, several of which are monotypic. Linnaeus (1758:322) included all members of the Tetraodontoidei (here considered to be a suborder of plectognath fishes with a median suture in each jaw; see Fraser-Bunner (1943:6) for a comprehensive diagnosis of the suborder) in a single genus, *Tetrodon,* a practice followed with few exceptions by Günther (1870:269). At the other extreme, Fraser-Brunner (1943:2-3) subdivided the teraodontoid fishes (his division Tetraodontiformes) into five families: Lagocephalidae, Canthigasteridae, Chonerhinidae, Tetraodontidae, Colomesidae, of which ". . . the Conthigasteridae is particularly well marked".

Recent literature (Bailey et al. 1960:49 and 1970:63; Norman 1966: 571; Lagler, Bardach, and Miller 1962:48; Böhlke and Chaplin 1968:685-686; Greenwood, Rosen, Weitzman, and Myers 1966:403) has tended toward the recognition of but a single family of western Atlantic and eastern Pacific pufferfishes, the Tetraodontidae, which is sometimes subdivided into subfamilies. However, on the basis of both osteological and external characters to be discussed, I feel that the Canthigasteridae or sharp-nosed puffers should maintain family status at least for present purposes and they are so treated herein. This opinion has been held by Tyler (1967:54), Randall (1968:280), and Herald (1961:276), although recently Tyler (personal communication) has modified his opinion, and believes the sharp-nosed puffers probably should be included as a subfamily of the Tetraodontidae.

There appears no justification for erecting additional families for the Atlantic genera of tetraodontoid fishes.

KEY TO FAMILIES OF PUFFERFISHES OF THE ATLANTIC OCEAN

A. Lateral lines inconspicuous, visible only with magnification. Nostrils and nasal papillae minute. Dorsal surface posterior to orbits distinctly keeled. Sphenotics excluded from cranial roof by frontals ..... Canthigasteridae

AA. Lateral lines easily visible without magnification. Nostrils and nasal papillae variously structured, but well developed and evident. Dorsal surface from interorbital area to dorsal fin not keeled. Sphenotics included in cranial roof ..... Tetraodontidae

FAMILY CANTHIGASTERIDAE

The Canthigasteridae represents a highly specialized branch of tetraodontoids, characterized by an extreme reduction of the lateral line and nasal organs. The mesethmoid is elongate and narrow anteriorly, a character which gives the snout its distinctive shape, and hence the designation of the group as "sharp-nosed" puffers. The sphenotics are excluded from the cranial roof by the frontals. I have not studied the vertebral osteology of this group, but detailed osteological analysis is under study by James C. Taylor of the Lerner Marine Leboratory, Bimini, Bahamas. His preliminary opinions support consideration of these fishes as distinctive, but only at the subfamily level.

A complete systematic treatment of the Atlantic representatives of the sharp-nosed puffers may necessarily entail revision of interoceanic and Indo-Pacific members of this family. For this reason, and because this is a separate, albeit closely related group, the sharp-nosed puffers are excluded from further discussion.

FAMILY TETRAODONTIDAE

The Tetraodontidae is a predominantly tropical, marine family of highly specialized plectognath fishes, which retains an extensive lateral line system and well developed nasal organs. About 90 species are recognized, the majority of which are Indo-Pacafic and poorly known (Tyler 1964:126). All have a median suture of both the upper and lower coalesced teeth, the character from which the family receives its name. Great variation among genera exists in the osteology of the skull, but the sphenotics are included in the cranial roof of all species. The Indo-Pacific genus *Xenopterus* Troschel has the sphenotics secondarily roofed by the frontals. This and the closely allied genus *Chonerhinos* Bleeker are sometimes recognized as a separate family, Chonerhinidae, characterized by an extremely high dorsal fin ray count of 25-38 and other features (Fraser-Brunner 1943:16).

Four genera of the Tetraodontidae are present in the Atlantic Ocean: *Colomesus, Ephippion, Lagocephalus,* and *Sphoeroides.* Although each is treated individually in later sections, some historical notes regarding relationships within the family are discussed here.

The genus *Tetraodon* Linnaeus was first subdivided by Swainson (1839:194). Despite the high incidence of inaccuracy and inadequate description in this work, the law of priority requires consideration of his genera. Five genera were proposed within Swainson's subfamily Tetraodinae: *Tetraodon, Leiodon, Lagocephalus, Cirrhisomus,* and *Canthigaster. Leiodon* and *Canthigaster* were emended later in the text (p. 328) to *Leisomus* and *Psilonotus* respectively, but page priority requires consideration of the first names inasmuch as these are accompanied by descriptions. The genus *Tetraodon* Linnaeus was assigned four species by Swainson: *T.*

lineatus Bloch, *T. testudineus* Bloch, *T. maculatus* Hamilton, and *T. fluviatilis* Hamilton. The first revisor, Bonaparte (1841: second page of *Lagocephalus* section), chose *T. lineatus* Bloch as the type-species with this statement: "*Tetraodon*, L. breve di capo, coperto di spine, qual' e il *lineatus* di Bloch". However, the *T. lineatus* of Bloch and that of Linnaeus do not appear to be conspecific (Bloch's *lineatus* appears to be an Indo-Pacific *Arothron*, while that of Linnaeus relates to a distinctive fresh water species from the Nile).

Jordan (1917:15) originally accepted *testudineus* as the type-species of *Tetraodon* on grounds of "justice and convenience", an action which would require *Sphoeroides* to be treated as a junior synonym. He later corrected himself (p. 167), noting that Swainson had advised Bonaparte to designate *T. lineatus* Bloch as the type-species of *Tetraodon*. Therefore, neither *lineatus* nor *testudineus* would be allowed to stand either on the basis of Bonaparte's revision of Swainson, or on subsequent revisions by other authors.

Fortunately, the type-species of *Tetraodon* was selected before Swainson subdivided the genus. In the "Dictionnaire Classique d'Histoire Naturelle", Lesson (1830:199) designated *Tetraodon lineatus* Linnaeus as the type-species: "Le type du genre est le Fahaca des Arabes (*Tetraodon lineatue*, L.) decrit par Geoffroy Saint-Hilaire . . ."

The genus *Leiodon* (=*Leisomus*) of Swainson included two species, *Tetrodon laevissimus* Bloch and Schneider, and *Tetrodon marmoratus* Hamilton, the former chosen by Bonaparte (1841:second page of *Lagocephalus* section) as the type-species. However, Bloch and Schneider (1801) described no species as *T. laevissimus*. Swainson cited no page or figure number after the Bloch and Schneider reference (although all of Swainson's other references include page or figure citations), indicating that he was probably acting with secondhand knowledge in his designation. Therefore, *T. marmoratus* Hamilton must be accepted as the type-species of the genus *Leiodon*. The *T. laevissimus* referred to by Swainson may have been confused with *Crayracion laevissimus* of Bleeker, after Klein (1744:18), which has been considered a junior synonym of *Tetrodon spengleri* Bloch by Norman (1966:572), or of *Tetrodon maculatus* Bloch and Schneider by Gill (1892:710). *Tetrodon spengleri* Bloch and *T. maculatus* Bloch and Schneider are congeneric species of *Sphoeroides*, thus *Leiodon* and *Leisomus* at times have been placed in synonmy of *Sphoeroides* Anonymous. Gill (1892:710) suggested that Swainson copied the error from the Regné Animal of Cuvier (1829). He further stated that the *T. marmoratus* of Hamilton is a substitute for *T. cutcutia* of Hamilton. If this is the case, then the genus *Leiodon* Swainson 1839 replaces *Chelonodon* Müller 1841. In any case, *Leiodon* must be removed from the synonymy of *Sphoeroides*, where it erroneously has been placed by recent authors (Fraser-Brunner 1943:10; Norman 1966:573).

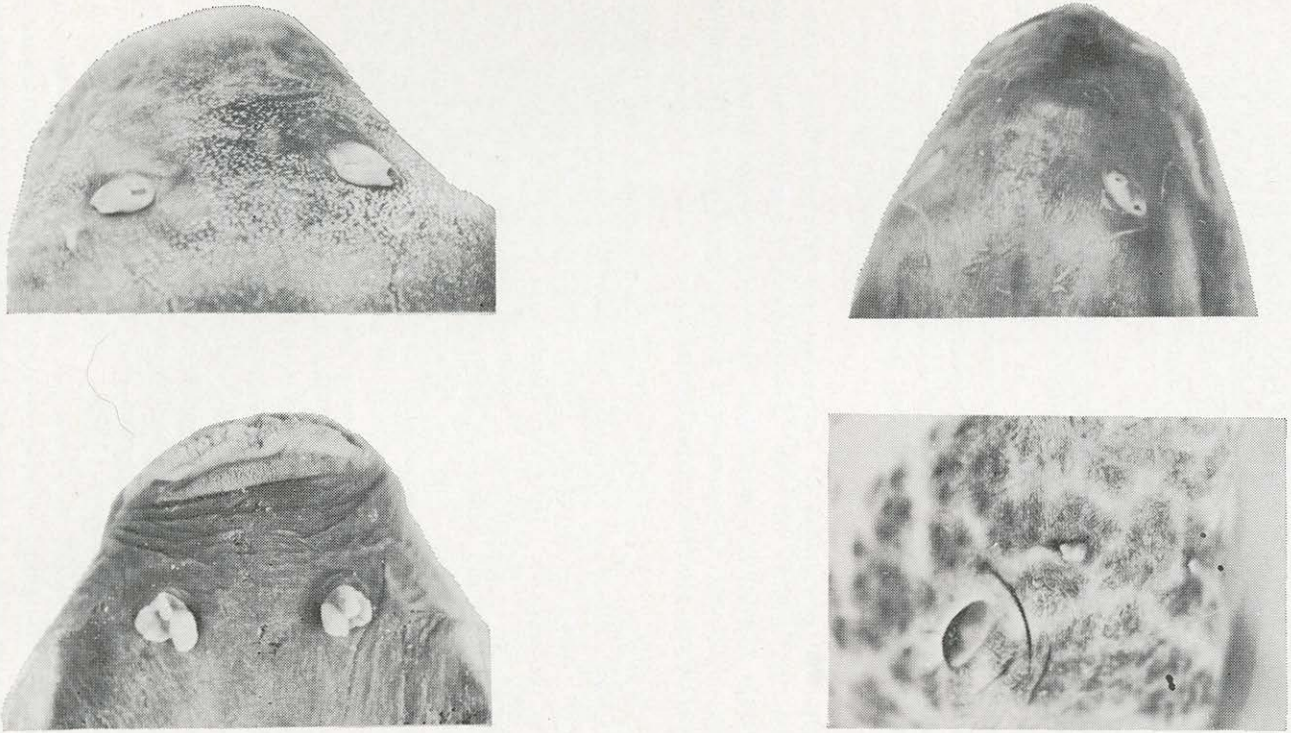

Figure 1. Nasal papillae of Atlantic genera of Tetraodontidae. Upper left: *Lagocephalus laevigatus* TABL 67-111, Honduras. Upper right: *Sphoeroides testudineus* ANSP 84658, Bahama Islands. Lower left: *Colomesus psittacus* RMNH uncat. Surinam. Lower right: *Ephippion guttifer* MRAC 80179, Angola.

Figure 2. Caudal fins of four species representing two genera of Tetraodontidae. Upper left: *Lagocephalus lagocephalus* BMNH Bournemouth, England. Upper right: *Lagocephalus laevigatus* TABL 67-111, Honduras. Lower left: *Sphoeroides dorsalis* ANSP 105185, Tobago. Lower right: *Sphoeroides spengleri* ANSP 104557, Colombia.

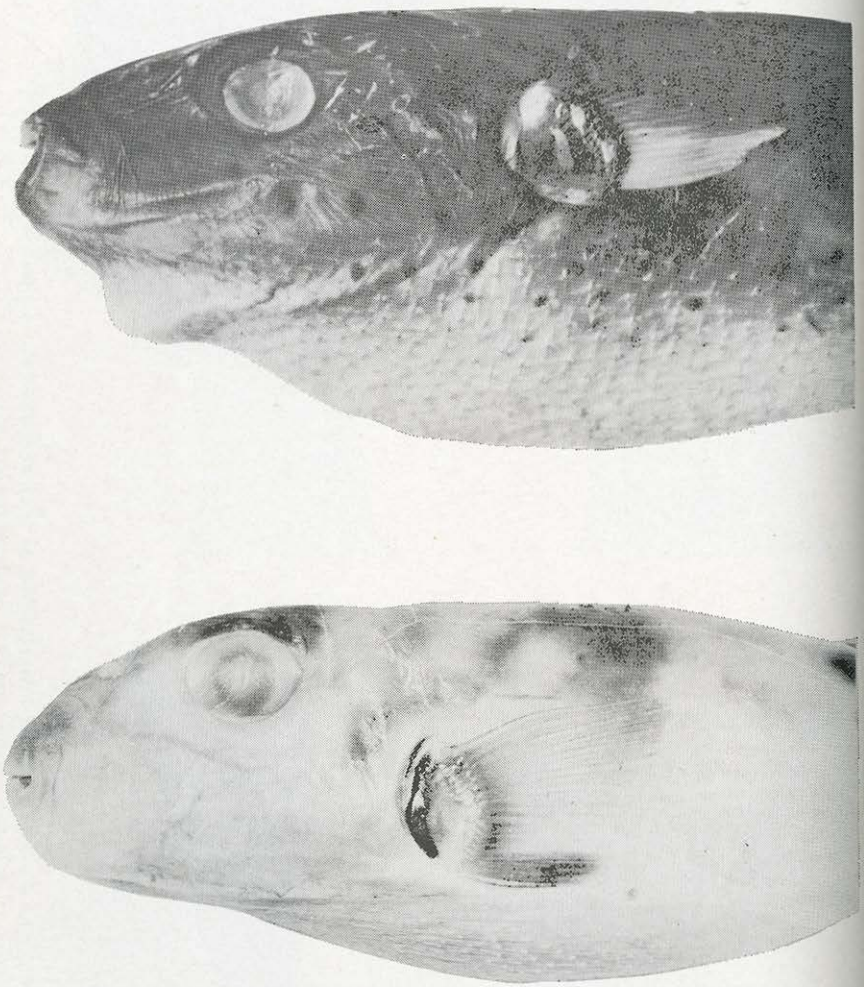

Figure 3. *Lagocephalus* species, illustrating interspecific diagnostic characters. Upper: *Lagocephalus lagocephalus* UMML 25026, Gulf Stream. (Note spotting of pectoral region, pigmentation of pectoral fin). Lower: *L. laevigatus* TABL 67-111, Honduras. (Note uniform pectoral region, pigmentation of pectoral fin and lateral line system).

Treatment of Swainson's *Lagocephalus* is included under the discussion of the synonymy of that genus.

Cirrhisomus included the species *Sprengleri* Bloch(sic), which is a misspelling of *spengleri* Bloch. This species is the type-species of the genus *Sphoeroides* Anonymous 1798, which has priority over *Cirrhisomus. Cirrhisomus* then becomes a junior synonym of *Sphoeroides.*

Canthigaster (=*Psilonotus*) is accepted as the correct name for the only genus in the family Canthigasteridae, and the type-species as selected by Bonaparte is *rostratus* Bloch, rather than the other originally assigned species, *electricus* Paterson.

Other later revisions of the tetraodontoids and related plectognaths that included references to Atlantic genera were those of Müller (1941), Bleeker (1865), Duméril (1855) from the manuscript of Bibron, Hollard (1857), Gill (1873, 1884, 1889, 1892), Jordon and Edwards (1886), Regan (1902), Fraser-Brunner (1943), and Le Danois (1959). Although monographic in design, this latter work contains numerous errors and competent authorities discount its value (Tyler 1963:203, 1965:122, 128; Greenwood, Rosen, Weitzman, and Myers 1966:345). While many generic names were proposed by these revisors, most eventually fell into synonymy under Swainson's genera or isolated generic names proposed even earlier. Exceptions include two of the Atlantic genera, *Ephippion* and *Colomesus.* The detailed history and systematics of all generic and specific names is treated in the appropriate sections of this paper.

Special mention should be made of the nineteenth century manuscript of Bibron. Only fragments of this work were ever published, and those in abbreviated form by Duméril (1855) and Troschel (1856). Examination of Bibron's types at the Museum National d'Histoire Naturelle in Paris has convinced me of the singular accuracy and insight of this scientist. I can only agree with Gill (1892:714) that "it certainly is not to the credit of French ichthyologists" that this work was never published. Had this been done, many of the subsequent systematic inaccuracies would have been eliminated.

KEY TO GENERA OF THE TETRAODONTIDAE OF THE ATLANTIC OCEAN

A. Nasal papilla a simple tube perforated by a pair of openings (Fig. 1); medial portions of body never encased in a bony corselet of irregularly shaped plates. Lateral ethmoids separated entirely by frontals.

B. Dorsal rays 7-9 or 13-15. Frontals included in the lateral margin of the skull, not excluded from this margin by large, recurved sphenotics.

C. Dorsal rays 13-15. Caudal distinctly lunate (Fig. 2). Posterior

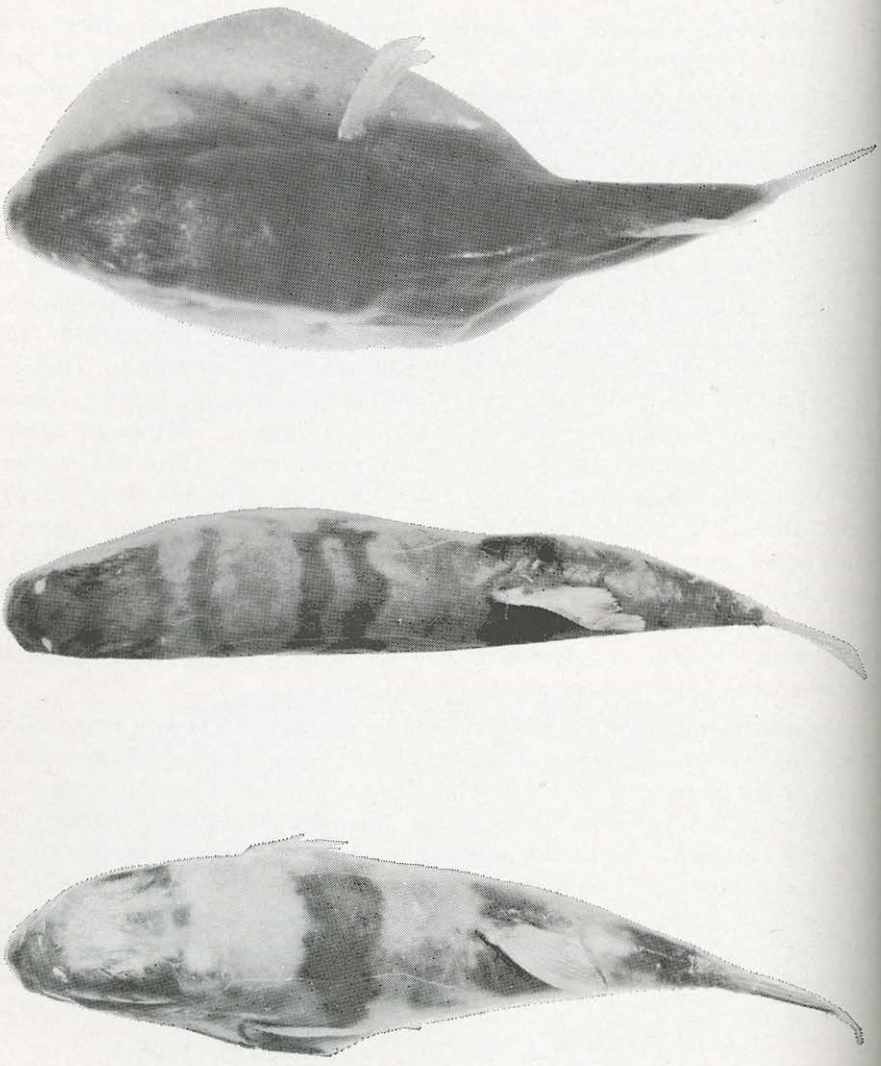

Figure 4. *Lagocephalus* species, illustrating variation in dorsal pigmentation. Upper: *L. lagocephalus* UMML 21888, off Africa. Juvenile-subadult dorsal pigmentation. Middle: *L. laevigatus* UMML 15765, off Africa. Typical eastern Atlantic dorsal pattern of juvenile-subadults. Lower: *L. laevigatus* TABL 67-111, Honduras. Typical western Atlantic dorsal pattern of juvenile-subadults.

limbs of frontals extend posterolaterally almost to upper end of post-temporals ..... *Lagocephalus*

CC. Dorsal rays 7-9. Caudal rounded, truncate, or with dorsal and ventral rays only slightly produced (Fig. 2). Posterior arms of frontals, if present, do not extend to near upper end of post-temporals ..... *Sphoeroides*

BB. Dorsal rays 10-12. Frontals totally excluded from lateral margin of the skull by enlarged, recurved sphenotics in adult specimens (more than 100 mm SL) or nearly so in smaller specimens ..... *Colomesus*

AA. Nasal papilla not a simple tube, but expanded to two lateral and one posterior flap (Fig. 1). In specimens more than 225 mm, irregularly shaped plates (bases of prickles and dermal spines) encase dorsal and lateral body surface between pectoral and dorsal fins in a bony corselet. Lateral ethmoids separated mostly by mesethmoid ..... *Ephippion*

GENUS *LAGOCEPHALUS*
Lagocephalus Swainson

Lagocephalus Swainson, 1839, pp. 194, 328. Type-species: *Tetrodon Pennantii* Yarrell (=*T. lagocephalus* Linnaeus), by subsequent selection by Bonaparte 1841.

Physogtser Müller, 1841, p. 252. Type-species: *Tetrodon lunaris* Bloch and Schneider, non *Physogaster,* Lacordaire, 1830, by subsequent selection by Jordan (1919:196).

Gastrophysus Müller, 1843, p. 330. Substitute for preoccupied *Physogaster* Müller, 1841. Type-species: *Tetrodon lunaris* Bloch and Schneider, by subsequent selection by Jordan (1919:196).

Promecocephalus (Bibron) Troschel 1856, p. 88. Type-species: *Tetrodon laevigatus* Linnaeus, by subsequent selection by Jordan (1919:262).

Pleuranacanthus (Bellanger) Bleeker 1865, pp. 59, 65. Type-species: *Pleuranacanthus argentatus* (Bibron) Duméril, by subsequent selection by Jordan (1919:262).

Discussion of Synonymy: Swainson's use of *Lagocephalus* (1839:194, 328) as a generic designation for one of his five subdivisions of the Linnaean genus *Tetrodon* predates all other systematic designations of this well defined group of fishes.

Lagocephalus was assigned two species by Swainson, *L. stellatus* Bloch and *L. Pennantii* Yarrell. Bonaparte (1841:second and third page of *Lagocephalus* section) selected the latter species, originally described as *Tetrodon Pennantii* by Yarrell (1836-37), as the type-species of *Lagocephalus.* Bonaparte simultaneously synonymized the earlier Linnaean

name, *Tetraodon lagocephalus,* under *Tetrodon Pennantii.* Tyler (1966: 603) surmised that Bonaparte was aware that his action in replacing the earlier *Tetraodon lagocephalus* of Linnaeus did not follow the law of priority, but preferred this action to adoption of the tautonymous scientific name, *Lagocephalus lagocephalus,* which would have resulted had he followed priority. It is necessary, therefore, to identify correctly *Tetrodon Pennantii* of Yarrell in order to determine the type-species of the genus *Lagocephalus,* and whether *Tetrodon Pennantii* is in fact a synonym of *Tetraodon lagocephalus* of Linnaeus.

Yarrell's original description of *Tetrodon Pennantii* is not wholly diagnostic in that some traits mentioned are characteristics of *L. laevigatus,* while others are of *L. lagocephalus.* His description is based on three specimens taken from Cornwall, England, none of which was designated as the type-specimen. His description specifically refers to the absence of stripes and spots; these are always absent in *L. laevigatus,* but absent only in large *L. lagocephalus.* However, the pectoral count of 14 and the presence of spines (prickles) arising from the "centre of four rays" appears to be diagnostic of *L. lagocephalus.* Yarrell's figure appears more like *L. lagocephalus,* especially the shape of the caudal fin and structure of prickles. It is possible that Yarrell had both species in hand, but much more likely that the absence of spots and stripes is indicative of older *L. lagocephalus* which have lost these characters. I have seen a number of *L. lagocephalus* from the British Isles, but no *L. laevigatus* north of Africa. Pennant (1776:132) originally had called the species *laevigatus,* and it was Pennant's editor who chose the specific name *lagocephalus* in a later (1812) edition. Yarrell synonymized Pennant's names under *T. Pennantii.*

Bonaparte's figure of *Lagocephalus Pennantii* is undoubtedly *L. lagocephalus,* as indicated by the four-rooted prickles, white lower portion of the pectoral fin, and elongate lower caudal lobe.

Therefore, as Tyler (1966:603) has correctly pointed out, Bonaparte's designation of *T. Pennantii* of Yarrell as the type-species of *Lagocephalus,* and his simultaneous and correct synonymization of *T. lagocephalus* Linnaeus with *T. Pennantii* Yarrell allows *lagocephalus* of Linnaeus to be considered the type-species of the genus *Lagocephalus* Swainson (article 69(a) (iv) of the International Code of Zoological Nomenclature).

Two years after Swainson named the genus *Lagocephalus,* Müller (1841:252) proposed the name *Physogaster,* with *Tetrodon oblongus* Bloch and *T. lunaris* Bloch and Schneider as examples. These Indo-Pacific species do not appear to be congeneric. However, Jordan (1919:196) selected *lunaris* Bloch and Schneider as the type-species for the genus *Physogaster,* and synonymized *Physogaster* with *Lagocephalus. Tetraodon lunaris* Bloch and Schneider is indeed congeneric with *T. Pennantii* Yarrell (=*lagocephalus* Linnaeus) the type-species of *Lagocephalus. Physogaster* would have been inadmissable in any case, as the name was preoccupied by the insect genus of Lacordaire (1830). Therefore, two years

later Müller (1843:330) replaced *Physogaster* with *Gastrophysus.*

In 1855, Auguste Duméril published a brief summary of part of Gabriel Bibron's manuscript dealing with the gymnodontid plectognaths. Eleven genera were listed in this summary, and although all generic names were set off from the rest of the text by being italicized, all were in vernacular French. Some were without diagnosis and recognizable only by the species assigned to them. Unfortunately, these assigned species were often manuscript names whose descriptions had never been published, and thus the genera are recognizable only by examination of specimens to which the manuscript names referred. The vernacular names were Latinized the following year by Troschel (1856:88). Four of the eleven generic names, *Promecocephalus, Geneion, Amblyrhynchotes,* and *Catophorhynchus,* have been included in the synonymy of *Lagocephalus,* and are discussed below.

Promecocephalus, originally Promécocéphale in the Duméril summary, was the first of Bibron's genera to include a diagnosis. Six species were listed as examples: "*T. argentatus,* Lacep., *lunaris* Schn., *spadiceus,* Richards, *lavigatus,* Lin., *Lagocephalus,* Bloch, non Lin. (l'espece decrite par ce dernier est un Rhynchote, Bib.), *inermis.* Schlegel" (Duméril 1855: 278). From this list of species, Jordan (1919:262) considered *laevigatus* as the type-species; however, all the listed species are considered congeneric by recent workers. Therefore, *Promecocephalus* (Bibron) Troschel must be retained as a junior synonym of *Lagocephalus.*

Geneion was included in Latinized form (but vernacular context) with a diagnosis in the Duméril summary. A single species, *maculatum* Bibron MS, was assigned to this genus. A description of this species has never been published, but the generic diagnosis (protruding lower jaw, prickles concealed by papillae) certainly is inapllicable to *Lagocephalus,* and is closed to *Amblyrhynchotes.* Le Danois (1959:189) had access to Bibron's types in the Museum National d'Histoire Naturelle in Paris, and synonymized *Geneion maculatum* with *Geneion honckenii* (Bloch) and thus considers *Geneion* as the genus to represent this latter species rather than *Amblyrhynchotes* which generally is used by recent workers who follow Fraser-Brunner's system (1943). In any case, *Geneion* is not a junior synonym of *Lagocephalus* as suggested by Jordan (1919:262). Fraser-Brunner (1943:9), and Norman (1966:572).

Amblyrhynchotes, originally Amblyrhynchote in the Duméril summary, had its type-species, *honckenii* Bloch designated by Jordan (1919: 263). This genus was subsequently synonymized with *Lagocephalus* by Norman (1966:572). However, *honckenii* Bloch is an Indo-Pacific species certainly not congeneric with *Lagocephalus,* and *Amblyrhynchotes* has been considered a valid genus by Fraser-Brunner (1943:2, 11).

Catophorhynchus, originally Catophorhynqué in the Duméril summary, was introduced with an inconclusive generic diagnosis. Two un-

described species, *C. lampris* and *C. longispinis* (both manuscript names), were assigned to it by Bibron (in Duméril 1855:280). Jordan (1919:262) and Fraser-Brunner (1943:9) considered *Catophorhynchus* a possible synonym of *Lagocephalus,* while Norman simply listed *Catophorhynchus* in synonymy under *Lagocephalus.* Le Danois (1959:208) resurrected *Catophorhynchus,* and considered Bibron's *C. lampris* and *C. longispinis* as synonyms of *Tetrodon scaber* Eydoux and Soulet, which species she designoted as "genotype" of *Catophorhynchus.* Her figures (Fig. 174-176), pp. 208-209, based on Bibron's specimen of *C. longispinis,* leave no doubt that this species does not belong to the genus *Lagocephalus,* and thus *Catophorhynchus* must be removed from the synonmy of *Lagocephalus.*

In addition to the manuscript names of Bibron discussed above, another manuscript name, *Pleuranacanthus,* from an 1830 manuscript of Bellanger (deposited in the Museum National d'Histoire Naturelle, Paris) has been associated with *Lagocephalus.* This name was first published by Bleeker (1865:59, 65). Jordan assigned *argenteus* (=*argentatus*) Bibron as type-species and synonymized this species with *Tetrodon sceleratus* Forster, a species of *Lagocephalus.* Y. Le Danois (1961:472) synonymized *Pleuranacanthus argenteus* Bellanger under *Lagocephalus;* thus *Pleuranacanthus* (Bellanger) Bleeker is a junior synonym of *Lagocephalus.*

Diagnosis of *Lagocephalus*: Cranial features of *Lagocephalus* have been illustrated by Hollard (1857:plates). Regan (1902:293), Fraser-Brunner (1943:3) and LeDanois (1959:203). Comparison of intergeneric cranial characters shows that *Lagocephalus* is most closely related to *Sphoeroides,* an Atlantic genus, and *Torquigener,* an Indo-Pacific genus. *Lagocephalus* differs from both in the dimensions of the ethmoid, which is much broader than in *Sphoeroides,* and much longer than in *Torquigener.* The frontal bones of *Lagocephalus* possess prominent posterolateral extensions reaching or almost reaching the post-temporals. This character is not known in other tetraodontids. Possession of such extensions by the Molidae (along with the general cranial similarities of this family to *Lagocephalus*) has led Fraser-Brunner (1943:4) to suggest a primitive origin of *Lagocephalus,* not far removed from the in some ways primitive but in other ways highly specialized Molidae. No other cranial features of especial distinction appear in this genus.

Seventeen to nineteen (7-8 pre-caudal + 10-12 caudal) vertebrae are present, the last one or two with prominent zygopophyses that form a dorsal and a ventral transverse keel.

Dorsal and anal fins falcate, usually with 13 to 15 and 12 to 13 rays respectively; pectoral fins with 14 to 18 rays. Caudal fin lunate; a fleshy posterior extension of the caudal peduncle extends posteriorly well onto the base of the caudal fin (Fig. 2).

The dorsal segment of the lateral line system is distinct (Fig. 3). A preocular loop, present immediately below the nasal papillae, is formed

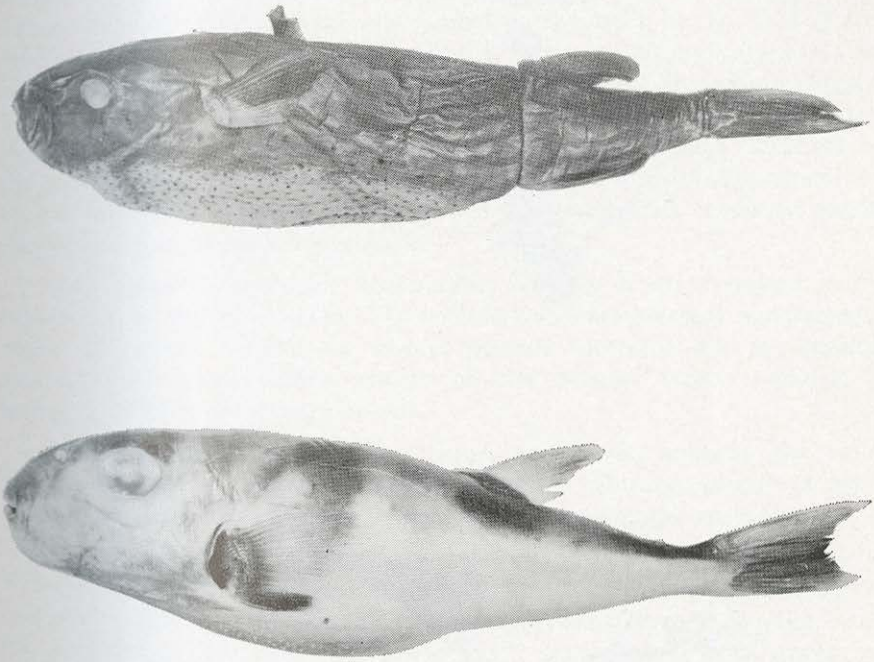

Figure 5. Atlantic species of *Lagocephalus*. Upper: *Lagocephalus lagocephalus* UMML 25056 (295 mm SL), Gulf Stream. Lower: *L. laevigatus* TABL 67-111 (139 mm SL), Honduras.

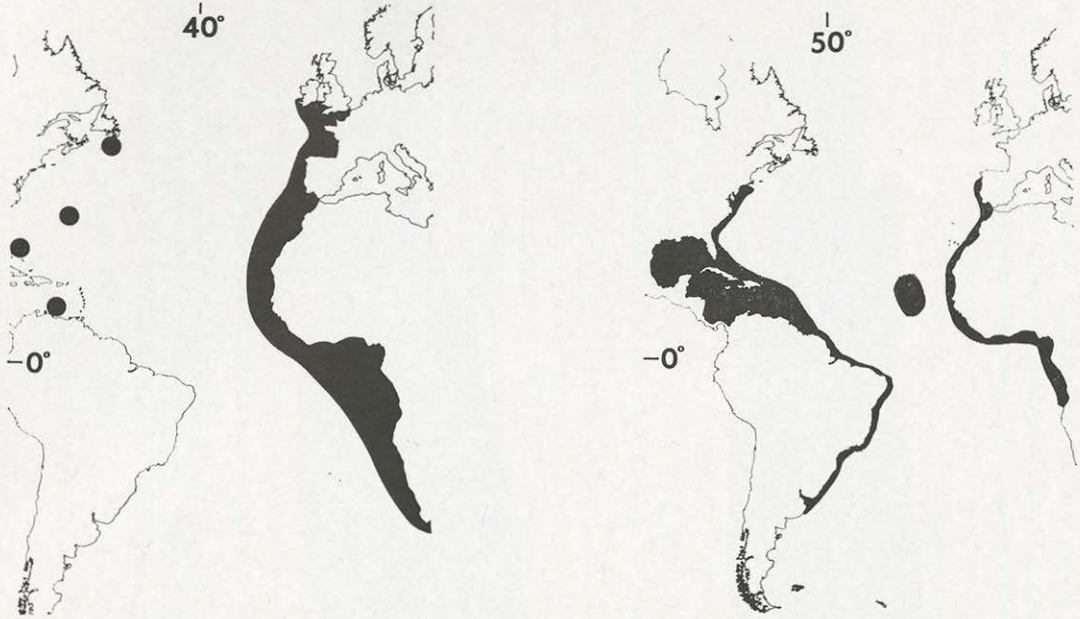

Figure 6. Distribution of Atlantic species of *Lagocephalus*. Left: *Lagocephalus lagocephalus*. Note records from isolated western Atlantic localities (Curacao, Gulf Stream, Bermuda, Newfoundland). Right: *L. laevigatus*.

from anterior extensions of the supraocular and subocular branches. These same branches meet again posterior to the orbits, and send branches posteriorly along the dorsum which arch downward at the level of the dorsal fin, and extend posteriorly to the termination of the caudal peduncle. An indiscrete branch extends from the postocular junction of the supraocular and subocular branches directly ventrad to the ventrolateral body angle. Extensions from the supraocular and dorsum branches meet just lateral to the occiput, and a transoccipital branch connects these junctions.

The ventral segment of the lateral line system is indistinct. A single branch on each side of the mouth extends from the level of the upper jaw ventrad onto the chin and extends caudad on the belly to the level of the pectoral fin, where it fades and disappears. I can see no posterior branches of the lateral line system which were mentioned and figured by Fraser-Brunner (1943:2, Fig. 3A). At best this portion of the system is represented by irregular vestiges of these branches. No ventral branches of the system are evident in specimens of *Lagocephalus lagocephalus* examined by me. However, this may be due to the excessively stiff, wrinkled condition of the skin of these individuals.

Nasal papillae are short broad tubes scarcely if at all raised above the surface of the snout (Fig. 1); each has an anteromedial and posterolateral aperture. Prickles are always present ventrally, but in Atlantic species they are only rarely present on the dorsum, which typically is smooth. Lappets are always absent.

Dorsal color is usually green, blue, or brown; laterally the color changes to silver. The ventral surface is white. Mottled, barred, or spotted markings are often present, with variation among the species.

Ecology and Distribution: *Lagocephalus* is the most pelagic and widespread genus of the Tetraodontidae. Species are found in all tropical and most temperate seas. In the Atlantic specimens have been taken from the northern British Isles near latitude 59° N., southward to Argentina near latitude 37° S.

KEY TO ATLANTIC SPECIES OF *LAGOCEPHALUS*

A. Pectoral rays 13 to 16 (Table 2). Dorsal fin far posterior, predorsal distance 2¼ or more times distance from dorsal fin origin to caudal fin base. In juvenile and subadults (to about 300 mm SL), dark blue or black spots on anterior and medial regions of belly, and laterally near pectoral fin base. In juveniles (to about 100 mm SL) about 9 dorsal bars of uniform width from orbits to dorsal fin insertion (Fig. 4). In adults, lower caudal lobe longer than upper (Fig. 2); lower third of pectoral white.

..... *Lagocephalus lagocephalus* Linnaeus

AA. Pectoral rays usually 17 to 18, rarely 15, 16 or 19 (Table 2). Dorsal fin not far posterior, predorsal distance less than 2¼ times (less

than 2 times in adults) distance from dorsal fin origin to caudal fin base. No spots laterally or ventrally. About 5 to 8 bars of various shapes and widths on dorsal surface, sometimes very faint or even absent especially in specimens from outside the tropics (Fig. 4). In adults, upper caudal lobe longer than lower (Fig. 2); pectoral uniformly dusky or with lower few rays dark.

..... *Lagocephalus laevigatus* Linnaeus

Lagocephalus lagocephalus (Linnaeus) Ocean Puffer
(Figs. 5 and 6)

Tetraodon (also *Tetrodon*) *lagocephalus* Linnaeus 1758:332 and 1766:410 (see following discussion). Bloch 1785:140 (description, diagnostic figure). Bloch and Schneider 1801:503 (brief but diagnostic description). Shaw 1804:441 (taken from Bloch). Pennant 1812:174 (England, editor amended from *T. laevigatus* of 1776 edition). Cuvier 1829:369 (after Linnaeus). Günther 1870:273 (diagnostic description, Africa, British Isles, Atlantic Ocean). Capello 1881:41 (Portugal). Guerin-Ganivet 1912:104 (Loire-Inferieure, English Channel, genus spelled *Tretodon*). Metzelaar 1919:168 (description, near Curacao, West Indies, from swordfish stomach) and 297 (Baie de l'ouest, Africa). Roule 1919:63 (Azores; Porto Santa, Madeira). Barnard 1927:966 (description, Atlantic, Mediterranean, Mauritius) and 1947:209 (diagnostic figure, South Africa).

Tetraodon laevigatus (not of Linnaeus) Pennant 1776 vol. III:132 (description, figure, England).

Tetrodon psittacus var. Bloch and Schneider 1801:505 (after Seba 1758, p. XXIII, f. 6).

Tetraodon (also *Tetrodon*) *stellatus* Donovon 1804:section dealing with pl. 66 (not of Bloch and Schneider, description, plate, England). Fleming 1828:115 (after Donovan, description). Jenyns 1835:31 (after Donovan).

Tetrodon Pennantii. Yarrell 1836:347 (description, figure, England). ? Capello 1873:87 (Angola, listing only, no diagnosis; possibly *L. laevigatus* which is common from Angola).

Lagocephalus Pennantii (also *Pennanti*). Swainson 1839:328 (assignment to genus *Lagocephalus*). Bonaparte 1841:unpaginated (review of Swainson's genera, synonymy of *Pennanti* with *Lagocephalus,* figure of *L. Pennanti*).

Promécocéphale lagocephalus (Bibron) Duméril 1855:277.

Promecocephalus lagocephalus (Bibron) Troschel 1856:88 (Latinized list of Bibron's names). Moreau 1881:72 (description, France).

Tetraodon janthinus Vaillant and Sauvage 1875:286 (original description, Hawaiian Islands).

Lagocephalus lagocephalus. Osorio 1890:59 (Angola). Jordan and Evermann 1898:1729 (tropical, reaching the coasts of southern Europe). Ramalho 1931:species 406 (description, diagnosis, figure, Atlantic and Mediterranean). Fowler 1936:1107 (West Africa and Bermuda). Fraser-Brunner 1943:10 (systematics of genus). Fowler 1944:302 (description of subspecies *L. l. nigrodorsum,* Pacific). Cadenat 1950: 285 (Mar du Senegal). Matheson 1950:193 (England). Smith 1950: 417 (S. Atlantic and Indian Oceans). Went 1950:1025 (Ireland). Rey 1952:254 (description, Spain, Mediterranean). Nunes 1953:221 (Madeira). Dollfus 1955:173 (Atlantic, Morocco). Le Danois 1959: 201 (systematics, Atlantic, in part). Bailey et al. 1960:49 (check list, Pacific). Gosline and Brock 1960:299 (Hawaii). Templeman 1962:811 (Newfoundland). Tyler 1964:124 (systematics) and 1966: 602 (establishment of type-species of genus). Liem and Scott 1966: 414 (after Templeman). Wheeler 1969:567 (description, stomach contents, England). Bailey et al. 1970:63 (check list, Atlantic-Pacific).

Lagocephalus oceanicus Jordan and Evermann 1903:425 (original description, figure, Hawaii).

Discussion of Synonymy: In his original description of *Tetraodon lagocephalus,* Linnaeus (1758:332) included a brief, non-diagnostic description: "abdomine aculeato, corpore laevi, humeris prominentibus". However, he cited four earlier references to the species: Linnaeus (1754) "Museum Adolphi Frederici" I. p. 59; Artedi (1738) "Genera" 58 and "Synonymia" 86; Linnaeus (1749) "Amoenitates Academicae" I. p. 310, t. 14, f. 4. idem.; and Gronovius (1756) "Museum Ichthyologicum". The first two references, and those to which they refer, indicate either a *Lagocephalus-* or a *Canthigaster*-like form. In the Amoenitates Academicae, however, although description and references are not diagnostic, the figure is definitely that of a sharp-nosed puffer, *Canthigaster.* The Gronovius reference is also to a species of *Canthigaster,* as shown by Tyler (1967:58). However, the work of Artedi almost doubtlessly refers to a *Lagocephalus.* A flow diagram (Fig. 7) illustrates the sequential references stemming from the original description of the species. No type of *T. lagocephalus* was found by Thunberg (1787) or Lönneberg (1896), so it is not possible to establish definitely what Linneaus had in mind. However, Bloch's (1787:140) figure of *T. lagocephalus* was diagnostic to species, and the species of Bloch has since been almost universally accepted as that intended by Linnaeus. Furthermore in his twelfth edition (1766:410), Linnaeus added a single reference to the four in his tenth edition. This was to Seba (1758) and definitely refers to *Lagocephalus lagocephalus.* Duméril (1855:279), in the summary of Bibron's manuscript, noted a difference between the *T. lagocephalus* of Linnaeus and of Bloch. However, because the intent of Linnaeus will probably never be known, and because *L. lagocephalus* (Linnaeus) is so widely known and accepted as the *lagocephalus* of subsequent authors, it appears logical to accept it as such, despite cer-

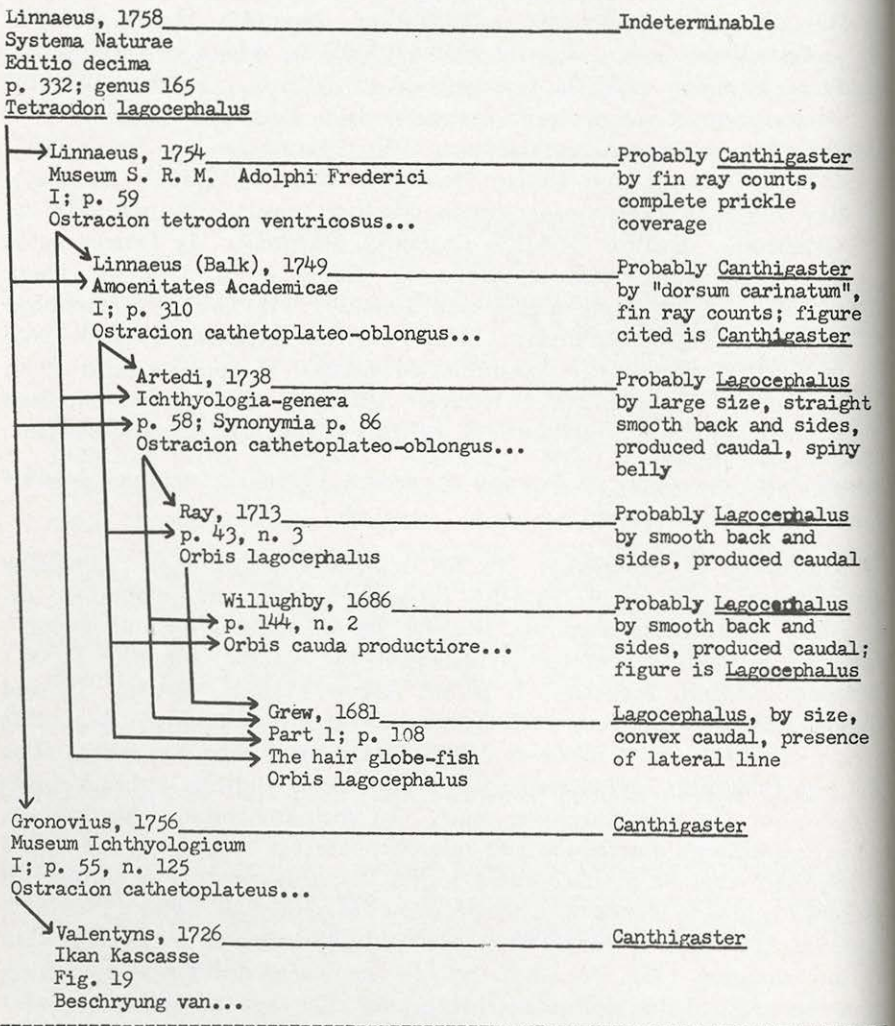

Figure 7. Flow diagram summarizing references (with annotations) associated with the original description of *Lagocephalus lagocephalus.*

tain discrepencies between *L. lagocephalus* and the original description in regard to fin ray counts, distribution, etc. Also, it should be remembered that much of the early study material was poorly preserved.

The above synonymy may overlook junior synonyms of *L. lagocephalus* based on specimens from outside the Atlantic Ocean. This species is one of the few Atlantic tetraodontids known to be interoceanic, and it likely has been treated in the literature on Indian Ocean and Pacific fishes.

Material Examined: Twenty-one series, 28 specimens.

Types: MNHM 3488 (1, 378), Cap de Bonne Esperance, type-specimen of *Promecocephalus* (Bibron). Troschel. MNHIM 9007 (1, 153) Hawaii; type-specimen of *Tetraodon janthinus* Vaillant and Sauvage. ANSP 70284 (1, 66), 17° 21' N., 103° 33' W., off western Mexico ANSP 70285 - 70286 (2, 86-114), 18° N., 105° 47' W., S.W. of Colima, western Mexico; and ANSP 70287 (1, 212), Socorro Island, Revillagigedo Islands, Mexico, all paratypes of *Lagocephalus lagocephalus* subsp. *nigrodorsum* Fowler. UNSP 50820 (1, 100), Hawaii; holotype of *Lagocephalus oceanicus* Jordan and Everman. **Western Atlantic:** RMNH 9852 (1,64), West Indies. UMML 7935 (1, 63), Gulf Stream off Miami. UMML 25056 (1, 295), Gulf Stream (off Miami?). FRBC (1,510), southeast coast, Newfoundland. **Eastern Atlantic:** UMML 21888 (1, 39), 0° 54'-01° 05' N., 4° 53'-51' E., Gulf of Guinea. BMNH (6, 22-34), 20° N., 22° 53' W. BMNH (1, 300), Mogadore, Morocco. BMNH (1, 267), Azores. BMNH (1, 428), Weymouth, England. BMNH (1, 350), Bournemouth Pier, England. **Indian Ocean:** BMNH (1, 44), Zanzibar. MNHN 2177 (1, 77, Le Reunion. **Pacific Ocean:** BMNH (1, 205), Tahiti. ANSP 87883 (3, 180-213), Abingdon I., Galapagos.

Diagnosis: Among Atlantic teraodontids, only the congeneric *Lagocephalus laevigatus* could be confused with *L. lagocephalus.* Falcate dorsal and anal fins with high fin ray counts (13-15, 11-14, respectively), the streamlined silvery body, and the strongly lunate caudal immediately separate *Lagocephalus* from other Atlantic tetraodontids. *Lagocephalus lagocephalus* differs from *L. laevigatus* in several morphological characters: *L. lagocephalus* has a more extreme posterior placement of the dorsal and anal fins (snout to dorsal origin about 78% of SL, compared to 66% in *L. laevigatus*); juveniles are especially distinct with dark spots near the pectoral base and adjoining ventral region, and nine uniform dorsal bars (Fig. 4). It has the lower caudal lobe longer than the upper (Fig. 2), the reverse condition is found in *L. laevigatus,* and the lower third of the pectoral white (pectoral uniformly pigmented or lower third is dark in *L. laevigatus*).

General Description (Tables 2-5): Head of adults moderate, 2.7 to 3.5 in SL, longer in subadults. Snout 2.2 to 2.5 in head, eye 5 to 7 in head, slightly larger in subadults. Least bony interorbit very broad, flat, 1.1 to 1.5 in snout, about 3 in head. Dorsal and anal nearly equal, 0.7

to 1.0 in snout, about 2.0 in head, and nearly opposite each other. Caudal moderately forked, medial caudal rays about equal to snout, and more than half (about 5/8) of longest (lower) caudal ray. Pectoral length about 0.8 in snout, 1.7 in head. Dorsal rays 13 to 16. Caudal rays 11, with the first upper ray and lower two rays unbranched.

Coloration exhibits strong countershading. The dorsum is a rich, dark green, brownish grey, or blue. In juveniles (to about 150 mm SL) nine darker bars occur on the dorsum, nearly uniform in width and spacing (Fig. 4); the first extends between the orbits, the last is at the insertion of the dorsal fin. A faint darkening between the nasal papillae gives indication of still another bar. About the level of the dorsal margin of the orbit, the dorsal pigmentation fades abruptly to silver (light grey in preservative) which extends ventrally to the ventrolateral body angle. The belly is white except for dark blue, brown, or black spots near the pectoral base (in specimens to about 300 mm SL) which extend onto the ventral surface. Spots and bars tend to fade in larger specimens. The caudal is heavily pigmented except distal extremeties; other fins are darkly pigmented with the lower third of the pectoral white.

Lappets are absent. Prickles are present on the belly only, and extend from just posterior to the chin to slightly anterior of the anus. Prickles are stout and arise from a four-pronged base. In adults they are not close-set, but spaced 4 or 5 mm apart.

This species attains at least 600 mm (about two feet) in total length. Sexual maturity is attained between 200 and 300 mm SL.

Geographic Variation: Because of the limited number of study specimens available, geographic variation and individual variability were indistinguishable.

Ecology and Distribution: *Lagocephalus lagocephalus* is probably the most pelagic of any tetraodontid. Limited collections indicate that specimens are normally taken far off shore, often in major oceanic currents, or at great depths. Several small specimens have been taken from tuna and swordfish stomachs (Metzelaar 1919:168, and material examined), and one very small specimen was taken by the R/V Pillsbury in an Isaacs Kidd midwater trawl pulled at 1000-1500m in water 2430 fms. in depth (but capture of this specimen could well have occurred during the trawl lift). Specimens taken near shore have apparently been in distress and carried by current to the colder limits of their range (Templeman 1962: 811; Wheeler 1969:568).

Food habits are poorly known; however, Wheeler (1969:568) noted the presence of numerous squid beaks in the stomachs of British specimens, along with fishes, crustaceans, and unidentified debris. He also mentioned that scars from squid suckers frequently occur on the body skin.

Lagocephalus lagocephalus is known from both coasts of the Atlantic; from England and Ireland in the eastern North Atlantic, from all of West

Africa and around Southern Africa to Natal, and from Newfoundland to Curacao in the western Atlantic (Fig. 6), as well as from the Mediterranean Sea, Pacific and Indian Oceans.

Lagocephalus laevigatus (Linnaeus) Smooth Puffer
(Figs. 5 and 6)

Tetraodon (also *Tetrodon*) *laevigatus* Linnaeus 1766:411 (original description, see following discussion). Schöpf 1787:189 (Rhode Island). Lacépède 1798:497, 500 (vernacular). Bloch and Schneider 1801:506 (description, Carolinas, after Linnaeus). Shaw 1804:446 (Carolinas, from previous authors). De Kay 1842:329 (diagnostic description, systematic history, New York). Storer 1846:241 and 1867:224 (Masachusetts). Poey 1868:431 (description, Cuba). Günther 1870:274 (description, Brazil, Gulf of Mexico). Gill 1873:15 (North America). Uhler and Lugger 1876:73 (description, Maryland). Yarrow 1877: 204 (Beaufort, North Carolina). Rochebrune 1882:178 (Senegal). Steindachner 1894:90 (Liberia). Boulenger 1903:188 (Guinea). Pellegin 1914:86 (Bauritania, West Coast of Africa). Metzelaar 1919: 298 (description, West Africa).

Tetraodon (also *Tetrodon*) *curvus* Mitchill 1815:472 (original description, of juvenile, New York). De Kay 1842:328 (copied from Mitchill, De Kay suspected this species to be the young of *T. laevigatus*). Storer 1846:242 (North America).

Tetrodon mathematicus Mitchill 1815:474 (original description, New York).

Tetraodon pachycephalus Ranzani 1840:73 (original description and figure, Brazil). Metzelaar 1919:169 (Venezuela).

Holacanthus melanothos (Gronovius) Gray 1854:23 (original description, Carolinas).

Promécocéphale laevigatus. (Bibron) Duméril 1855:277 (vernacular publication of Bibron's manuscript).

Promecocephalus laevigatus. (Bibron) Troschel 1856:88 (Latinization of Bibron's generic manuscript name).

Apsicephalus (*Promecocephalus*) *laevigatus.* Hollard 1857:plates (osteology).

Gastrophysus laevigatus. Bleeker 1863:22 (description, figure).

Tetrodon lineolatus Poey 1868:432 (original description, of juvenile, Cuba).

Lagocephalus laevigatus. Abbott 1868:827 (New Jersey). Jordan and Gilbert 1878:366 (Beaufort, North Carolina, sight records only). Goode 1879:109 (St. Johns River, Florida). Goode and Bean 1879: 122 (Pensacola, Florida). Jordan and Gilbert 1883a:305 (Galveston, Texas). Jordan and Gilbert 1883b:619 (Charleston, South Carolina).

Jordan and Gilbert 1883c:860 (North America). Jordan 1886b:605 (West Indies). Jordan and Edwards 1886:232 (syonymy, description, Cape Cod to Brazil). Buettikofer 1890:480 (Liberia). Osorio 1890: 59, 200 (Angola). Berg 1895:82 (synonymy, description, Montivideo, Uruguay). Jordan and Evermann 1898:1728 (synonymy, description, figure, Cape Cod to Brazil). Evermann and Marsh 1899:266 (key, description, figure, Puerto Rico). Gilbert 1900:176 (Maceio, Brazil). Wilson 1900:355 (Beaufort, North Carolina). Evermann and Kendall 1907:105 (Argentina). Smith 1907:348 (synonymy, ecology, North Carolina). Sumner, Osburn, and Cole 1911:762 (Woods Hole, Massachusetts). Ehrenbaum 1915:79 (Kamerun). Ribeiro 1915: second page of Tetraodontidae section (key, description, Brazil). Latham 1917:22 (Long Island). Fowler 1919a:287 (Angola) and 1919b:14 (New Jersey). Lahille 1921:30 (Argentina). Beebe and Tee-Van 1928:263 (Haiti). Meek and Hildebrand 1928:811 (not reported as this species from Panama, description compiled from other accounts, see record under *L. pachycephalus*). Devincenzi 1924:246 (Rio de la Plata, Uruguay). Chabanaud and Monod 1927:287 (Mauritania). Ramalho 1931:species 407 (description, figure, North Atlantic). Nichols and Breder 1934:139 (New England). Pozzi and Bordale 1935:177 (Argentina to 38° S.). Fowler 1936:1107 (synonymy, key, description, figure, West Africa). Fowler 1941:182 (Brazil). Longley and Hildebrand 1941:299 (Tortugas, Florida). Baughman 1943:212 (Texas, as prey of lutjanid). Fraser-Brunner 1943:10 (systematics of genus). Irvine 1947:216 (Gold Coast). Breder 1948:231 (key, description, figure). Schultz 1949:197 (synonymy, synonymizes *T. pachycephalus* under *L. laevigatus,* Venezuela). Cadenat 1950: 285 (Senegal). Hildebrand 1954:320 (ecology, Texas and Yucatan). Hildebrand 1955:218 (ecology, Campeche, Yucatan). Wiebazahn 1955:248 (synonmizes *T. pachycephalus* of Metzelaar under *L. laevigatus,* Venezuela). Boschung 1957:562 (Alabama). Briggs 1958:299 (Atlantic, based on previous authors). Wheeler 1958:246 (historical account of type). Poll 1959:340 (description, figure, tropical Atlantic). Bailey et al. 1960:49 (check list, Atlantic). Gordon 1960:78 (Rhode Island). Ringuelet and Aramburu 1960:52 (Argentina). Springer and Woodburn 1960:89 (ecology, Tampa Bay). Ribeiro 1961:5 (Rio de Janeiro). Yerger 1961:115 (Alligator Harbor, Florida). Bullis and Thompson 1965:61 (catch records). Daget and Iltis 1965:57 (Bay of Cocody, Ivory Coast). Miller 1965:103 (ecology, Texas). Parker 1965:218 (annotated check list, Texas). Roithmayr 1965:20 (Gulf of Mexico). Cervigon 1966:837 (description, ecology, Cubagua, Venezuela). Gines and Cervigon 1968:38, 44, 71, 80, 82 (ecology, Guayanas, Surinam). Bailey et al. 1970:63 (check list, Atlantic). Franks et al. 1972:126 (ecology, Mississippi).

Lagocephalus pachycephalus. Jordan and Rutter 1897:128 (description, Jamaica). Jordan and Evermann 1898:1728 (description, Jamaica,

after Jordan and Rutter). Ribeiro 1915:third page of Tetraodontidae section (key description, Brazil). Fowler 1917:136 (Panama). Meek and Hildebrand 1928:810 (key, description, Panama). Fowler 1931a: 405 (Trinidad). Beebe and Tee-Van 1933:245 (Bermuda). Puyo 1949:249 (French Guiana). Briggs 1958:299 (Western Atlantic, Gulf of Mexico, based on previous authors). Bailey et al. 1960:49 (check list, Atlantic).

Lagocephalus guntheri Ribeiro 1915:third page of Tetraodontidae section (original description, Brazil).

Lagocephalus lagocephalus. Le Danois 1959:201 (Atlantic, systematics, in part).

Discussion of Synonymy: Linnaeus, in the twelfth edition of "Systema Naturae", added a sixth species, *T. laevigatus,* to the genus *Tetraodon* (spelled *Tetrodon* in the twelfth edition). The brief original description of this form was nevertheless diagnostic, especially the fin ray counts, and there has been since relatively minor systematic difficulty with this species. Juveniles often have a strikingly barred pattern on the dorsum which has led some early authors to consider them as distinct. However, examination of adequate series of subadults reveals a gradual loss of this character with age.

Lagocephalus pachycephalus (Ranzani) is the junior synonym most frequently seen in the literature. This form, presumably tropical, purportedly has a shorter, more blunt head than that of *L. laevigatus.* All specimens identified as this species which I have examined fall within the morphological variation of *L. laevigatus,* as does the original description and figure of Ranzani (1840:73). Therefore, I see no reason not to consider *L. pachycephalus* as a junior synonym of *L. laevigatus,* as has been done by Schultz (1947:197) and Wiebazahn (1955:248).

Lagocephalus guntheri Ribeiro was considered distinct from *L. laevigatus* because of the presence of prickles on the dorsum (Ribeiro, 1915: third page of Tetraodontidae section). Prickle patterns are extremely variable in some teraodontid species, and as no other consistent differences appear in those Brazilian specimens with a prickled dorsum, *L. guntheri* is considered a junior synonym of *L. laevigatus.*

Material Examined: Forty-eight series, 67 specimens.

North America: MNHN 3512 (1, 274), South Carolina. FSU 3714 (1, 310), 10880 (1, 258), 15568 (1, 312), 17522 (skull), UMML 5338 (1, 98), NMFS-G (1, 221), USNM 39351 (1, 520), Florida. NMFS-G BT 16, E7 (1, 165), off Louisiana. NMFS-G Gus 20 W61 (2, 113-132), off Vera Cruz, Mexico. **Central America:** UMML 1803 (1, 74), off Campeche, Mexico. TABL 67-111 (2, 162-169), 67-98 (1, 37), off Honduras. ANSP 49835 (1, 233), Colon, Panama. **South America:** UMML 13987 (1, 130), RMNH 16342 (1, 91) RMNH (1, 190), (1, 191), (1, 103), off Surinam.

ANSP 100100 (1, 180), off Parnaiba, Brazil. MZUSP 7667 (1, 161), 7669 (1, 38), 7670 (1,52) 7671 (1, 50), all off Aracaju, Sergipe, Brazil. BMNH (1, 163), Brazil. MZUSP 773 (1, 49), 927 (2, 52-71), 7672 (1, 138), Sao Paulo, Brazil. MZUSP 2362 (1, 93), Sao Francisco do Sul, Brazil. **West Indian Islands:** BMNH (1, 111), Jamaica. ANSP 75843 (1, 61), Vessigny, Trinidad. UPR 1389 (1, 215), 1395 (2, 47-54), 2936 (4, 31-37), Puerto Rico. **Africa:** BMNH (1, 180), Lagos. ANSP 103211 (3, 101-132), off Guinea. BMNH (2, 81-103), Accra, Gold Coast. UMML 15765 (3, 64.119), Gulf of Guinea MRAC 71541-71542 (2, 83-94), 77930-77931 (2, 41-119), MRAC 78787 (1, 36), MRAC 127758-127759 (1, 303), 119333 (1, 321), TABL 62-273 (8, 300-350), off Angola.

Diagnosis: *Lagocephalus laevigatus* differs from *L. lagocephalus* in the more anterior placement of its dorsal and anal fins (snout to dorsal origin about 66% of standard length, compared to 78% in *L. lagocephalus*), the absence of dark spots near the pectoral base or adjoining ventral region, and a variable dorsal pigmentation pattern, which never consists of nine uniform bars (Fig. 4). *Lagocephalus laevigatus* has the upper caudal lobe longer than or equal to the lower (Fig. 2), and a pectoral fin with uniform pigmentation, or with a slightly darker ventral or basal portion.

General Description (Tables 2-5): Head of adults 2.9 to 3.4 in SL, slightly longer in subadults. Snout 1.7 to 2.0 in head, eye about 4 to 4.2 in head. Least bony interorbit broad, flat, about 1.4 in snout and 2.5 in head. Dorsal and anal nearly equal and opposite, 0.8 to 0.9 in snout, about 1.7 in head. Caudal about 2/3 snout length and deeply forked, the medial rays usually less than 1/2 dorsalmost caudal rays. Pectoral length 1.0 to 1.2 in snout, 1.9 to 2.3 in head. Dorsal rays usually 13 or 14, rarely 15, anal rays 12 to 13. Pectoral rays 15 to 19, usually 17 or 18. Caudal rays 11, with the first upper ray and lower two rays unbranched.

The coloration exhibits strong countershading. The dorsum is dark green to brownish grey, occasionally with about five to eight irregular bars, especially distinctive in juveniles from more tropical regions (Fig. 4). These bars tend to be lost in adults. About the level of the orbit, dorsal pigmentation fades abruptly to silver (light grey in preservative), which extends ventrally to the ventrolateral body angle. The belly is white; often, rich black pigmentation is found anterior to the pectoral fin base. The caudal is heavily pigmented except its distal extremeties. Other fins are variably pigmented; the pectoral base or lower third of the pectoral often has heavy pigmentation.

Lappets are absent. Prickles are present only on the belly, except for rare individuals with prickles on the dorsum from the western South Atlantic. Prickles on venter extend from immediately posterior to the chin to well anterior to the anus. The strong prickles arise from a three-pronged base which may sometimes bear a fourth, subequal prong, and are moderately close set, spaced about 2 or 3 mm apart in adults.

This species attains at least 520 mm (about 21 inches) in total length, and perhaps a much larger size (pers. comm., Frank Schwartz). Sexually mature specimens between 200 and 300 mm SL have been examined.

Geographic Variation: Specimens from the coast of Africa have a slightly higher number of pectoral fin rays (M = 17.8, n = 36) than do western Atlantic populations (M = 16.8, n = 44). Juveniles from the eastern Atlantic tend to bear more numerous dorsal, irregular bars than do populations from the western Atlantic (Fig. 4). Juveniles of temperate populations in the western North Atlantic are most often without dorsal bars.

Ecology and Distribution: *Lagocephalus laevigatus* is found in both pelagic and inshore habitats; sometimes it is found even in the shallow waters of estuaries. Collections indicate that this is predominantly a tropical and temperate form. No specimens are known from the extreme depths inhabited by *L. lagocephalus,* but individuals are common to depths of 30 meters.

Lagocephalus laevigatus is known from both coasts of the Atlantic, from northern Africa to Angola in the eastern Atlantic, and from New England to Argentina in the western Atlantic (Fig. 6).

GENUS *SPHOEROIDES*

Sphoeroides Anonymous

Crayracion (Klein) Walbaum, 1792, p. 580. Type-species: *Tetrodon spengleri* of authors, by subsequent designation of Bleeker, 1865, 65. Name rejected, see discussion of synonymy.

Les Sphéroides, Lacépède, 1798, II:22. Type Le Sphéroide tubercule Lacépède (=*Tetrodon spengleri* Bloch).

Sphoeroides Anonymous, 1798, p. 676. Latinization of generic names of Lacèpéde. Type-species: Le Sphéroide tubercule Lacépède (=*Tetrodon spengleri* Bloch), by substitution of generic name.

Spheroides. Duméril, 1806, p. 342, after Lacépède. Type-species: Le Sphéroide tubercule Lacépède (=*Tetrodon spengleri* Bloch), by substitution of generic name.

Orbidus, Rafinesque, 1815, p. 90. Substitue for Les Sphéroides, Lacépède, and so takes the same type-species: Le Sphéroide tubercule Lacépède (=*Tetrodon spengleri* Bloch).

Sphaeroides, Pillot, 1831, p. 279, after Lacépède. Type-species: Le Sphéroide tubercule Lacépède (=*Tetrodon spengleri* Bloch), by substitution of generic name.

Cirrisomus Swainson, 1839, II:194, 328. Type-species: *Tetrodon Sprengleri* Bloch (misspelling of *spengleri*) by monotypy.

Chelichthyes Müller, 1841, p. 252. Type-species: *Tetrodon* (*Chelichthyes*)

pachygaster by subsequent monotypy Müller and Troschel (1848a: 677).

Anchisomus (Kaup) Richardson, 1854, pp. 156-169. Type-species: *Tetrodon spengleri* Bloch by subsequent designation by Jordan (1919:261).

Holocanthus, (Gronow) Gray, 1854, p. 24. Type-species: *Holacanthus leionothos* (=*Tetrodon testudineus* Linnaeus) by subsequent designation by Jordan (1919:258). Name preoccupied by *Holacanthus* Lacépède, 1803, a chaetodontid.

Stenometopus (Bibron) Troschel 1856, p. 88. Type-species: *Tetraodon testudineus* Linnaeus by subsequent designation by Jordan (1919:262).

Liosaccus Günther, 1870, pp. 272, 287. Type-species: *Tetrodon cutaneus* Günther (=*Tetrodon pachygaster* Müller and Troschel) by subsequent designation by Jordan (1919:357).

Thecapteryx Fowler, 1948, pp. 1-4. Type-species: *Thecapteryx lioderma* (=*Tetrodon pachygaster* Müller and Troschel) by monotypy.

Discussion of Synonymy: Crayracion is a pre-Linnaean name introduced by Jacob Klein (1744:18) in his "Historiae Naturales". In Klein's "Gesellshaft Schauplatz" (Vol. LV: 1777), Crayracion was again used, but as a polynomial: "Crayracion laevissimus ex terre rufescens." Walbaum (1792:580) included *Crayracion* under his "Nova Genera Kleinii". No species were listed therein, only the terse description "Der kropffisch. Corpus Strumosum". However, the International Commission on Zoological Nomenclature (1926:94) in opinion 21 has ruled that "When Walbum, 1792, reprinted in condensed form (but did not accept) the genera of Klein, 1744, he did not thereby give to Klein's genera any nomenclatorial status, and Klein's genera do not therefore gain availability under present Code by reason of being quoted by Walbaum." This followed the principle stated in the same article (pp. 91-92): "A pre-Linnaean name, ineligible because of its publication prior to 1758, does not become eligible simply by being cited or reprinted with its original diagnosis after 1757. To become eligible under the Code, such names must be reinforced by adoption of acceptance by the author publishing the reprint." Threfore, *Crayracion* must be rejectd as presented by Walbaum in 1792. Bleeker (1865:65) resurrected the name *Crayracion* and noted that the first named species by Klein in 1744 was *Tetraodon spengleri* of authors, or some closely related species. He went on to include all species with closed nasal tentacles in the genus. Jordan (1923:42) considered that Bleeker's mention of *T. spengleri* was sufficient to fix the type. However, Bleeker was apparently unfamiliar with *T. spengleri* of authors. There is little doubt that the first named species of Klein, which is well figured, was in fact *T. spengleri* Bloch. But this species does not have unperforated nasal tentacles which are given as the diagnostic character of the genus, *sensu* Bleeker. However, it is clear that Bleeker, under article 69 (a) iii of the International Code of Zoological Nomenclature, accepted and thus estab-

lished *T. spengleri* of authors as the type-species of *Crayracion,* because he stated that if the type of *Tetraodon* is not in a genus distinct from *Crayracion laevissimus* Klein (=*T. spengleri* Bloch), then *Crayracion* has priority over *Tetraodon* and should be substituted. Bleeker of course did not accept 1758 as the starting point of zoological nomenclature, and further did not consider *T. spengleri* to be generically distinct from other species of *Tetraodon.* As noted above, however, *Crayracion* has no nomenclatural status until the 1865 diagnosis by Bleeker.

The introduction of the colloquial name "Les Spheroides" into the literature by Lacépède, along with inadequate diagnosis and an inaccurately described type-specimen, caused extensive nomenclatural difficulty with this genus for more than a century.

In Lacépède's "Histoire Naturelle de Poissons" (vol. 2, p. 22) the following diagnosis is given: *Les Sphéroides*—Point de nageoires du dos, de la queue, ni de l'anus, quatre dents au moins a la machoire supérieure. To this genus was assigned only "le Sphéroide tubercule".

It appears as though this genus was based on a misinterpretation of one of Plumier's manuscript figures, the front view of which displays no dorsal or anal fin. Another figure of Plumier, representing the same fish, shows the pectoral fin arising anterior to the dorsal, which appeared to Lacépède as a hump. This figure was described by Lacépède as another species, of the genus *Tetrodon,* and named after Plumier, Le Tetrodon Plumier (Bloch and Schneider, 1801:509, 510 and Index:LVII; Cuvier, 1829:369; Gill 1889:607). It was on these misinterpretations of Plumier's drawings of what is now known as *Sphoeroides spengleri* that the genus had its origin. Subsequent authors from Rafinesque (1815:90) to Gill (1889:607 and 1892:708) have objected to admission of a generic name under such circumstances, but since the 1886 "Review of the American Species of the Tetraodontidae" by Jordan and Edwards, the generic name *Sphoeroides,* or one of its variant spellings (*Sphaeroides, Spheroides*) has been used most frequently to designate the many closely allied species of common Atlantic pufferfishes. Priority of the spelling *Sphoeroides* is based on the first Latinized publication of the term in an unsigned review of Lacépède's work in 1798. Subsequent spellings arose from later reviews or editions of Lacépède's work. Jordan (1923:240) was the first modern author to publish, in footnote, mention of the original spelling. Unfortunately, this note has been frequently overlooked; thus, the variant spellings continued. Shipp and Yerger (1969a:426) again noted the correct generic spelling.

Chelichthyes described by Müller (1841:252), remained devoid of species for seven years. Although authors in this century (Jordan 1917: 196, Norman 1966:573) have considered *T. testudineus* Linnaeus as the type-species, Tyler (1964:126-127) has clearly established *Tetrodon* (*Chelichthyes*) *pachygaster* Müller and Troschel as the type by subsequent

monotypy. *Sphoeroides pachygaster,* although one of the most atypical members of the genus, is considered congeneric. *Chelichthyes* (also spelled *Cheilichthyes* or *Chilichthyes*) is, therefore, a junior synonym of *Sphoeroides.*

Holacanthus is a generic name of chaetodontid angelfishes introduced in the literature in 1803 by Lacépède. In 1854 J. E. Gray edited the "Catalogue of Fish Collected and Described by Laurence Theodore Gronow" which contained manuscript names used by Gronow during the preceding century. The preoccupied name *Holacanthus* was herein used to include diodontids and tetraodontids, and Jordan (1919:258) considered the second named species, *Holacanthus leionothos,* as the type-species. From Gronow's description this species its very probably *S. testudineus,* which places *Holacanthus* Gronow as a junior synonym under *Sphoeroides.*

Among the numerous manuscript names of Gabriel Bibron, published in colloquial French by Duméril (1855) and Latinized by Troschel (1856), *Stenometopus* is clearly a junior synonym of *Sphoeroides.* I have examined Bibron's types in the Museum National d'Histoire Naturelle, Paris. The type-species is *Stenometopus testudineus* (Bibron) Duméril (=*Tetraodon testudineus* Linnaeus). Other type-specimens of *Stenometopus* examined and identified are: *Stenometopus spengleri* (Bloch) = *Tetrodon spengleri* Bloch, *S. marmoratus* (Lowe) = *Tetrodon marmoratus* Lowe, *S. laevissimus* (also type of *Tetrodon laevissimus* Cuvier, not of Klein) =? *Tetrodon* (*Cheilichthyes*) *pachygaster* Müller and Troschel, *S. bernierii* nov. sp. =*Terodon nephelus* Goode and Bean, *S. binummulatus* nov. sp. =*Tetrodon hispidus* var. *maculatus* (*Sphoeroides maculatus*) Bloch and Schneider, *S. latero-laevis* nov. sp. =*Sphoeroides greeleyi* Gilbert, *S. pleei* nov. sp. =*Tetraodon testiudineus* Linnaeus, *S. angusticeps* (Jenyns) =*Tetrodon angusticeps* Jenyns. No other types of *Stenometopus* of Bibron were found. All of the above species are considered congeneric, and species of *Sphoeroides* as here defined.

Other names occasionally placed in synonymy under *Sphoeroides* include *Leiodon* Swainson, 1839; *Uranostoma* (Ballanger) Bleeker 1865; *Guentheridia* Gilbert and Starks, 1904; *Lepidorbidus* Fowler, 1929; *Torquigener* Whitley, 1930; and *Omegophora* Whitely, 1934. *Leiodon* has been treated above.

Uranostoma is a manuscript name of Ballenger (often erroneously attributed to Bibron's manuscript), dating from 1830. Bleeker (1865:59) first published the name with mention of the type-species, and perhaps only species, *U. guttata* of Ballenger under *Tetraodon hypselogeneion* Bleeker. Jordan's designation of *Tetraodon testudineus* Linnaeus as the type-species is therefore invalid. *Tetrodon hypselogeneion* is generally included in the genus *Amblyrhynchotes* (Bibron) Troschel (Fraser-Brunner 1943:11). Thus, *Uranostoma* is not synonymous with *Sphoeroides.*

Guentheridia has as its type and only species the eastern Pacific *Tetro-*

don formosa Günther. Cursory examination of pigmentation patterns indicate affinities to *Sphoeroides annulatus,* a sympatric species. Validity of the generic distinctness of this species requires further study.

Lepidorbidus Fowler is an Indian Ocean genus from deep water (200 fathoms). Examination of the type-specimens of the type-species, *Sphoeroides marleyi* Fowler, reveals a form generically distinct from *Sphoeroides,* very probably an *Amblyrhynchotes.*

Torquigener, an Indo-Pacific genus, is considered by Fraser-Brunner (1943:12) as distinct from *Sphoeroides. Omegophora* has not been examined, but from the geographic range of the genus (western Pacific) congenerity with *Sphoeroides* is doubtful.

Diagnosis: Cranial features of *Sphoeroides* have been illustrated by Fraser-Brunner (1943:3) and Le Danois (1959:193, 198, 199). Comparison of intergeneric cranial characters shows that *Sphoeroides* is most closely related to *Lagocephalus,* a circumglobal genus, and *Torquigener* an Indo-Pacific genus. *Sphoeroides* differs from both in the very thin, fragile medial bones (frontals, ethmoids), compared with their broad, heavy homologues in the other genera. In addition, *Sphoeroides* lacks the extensive posterolateral extensions of the frontals found in *Lagocephalus,* and possesses a much more elongate mesethmoid than that of *Amblyrhynchotes. Sphoeroides* is apparently a specialized offshoot of the more generalized genus *Lagocephalus.*

Usually seventeen to nineteen (8 + 9-11) vertebrae are present, the last few without prominent zygopophyses. Dorsal and anal fins rounded to slightly falcate, usually with 8 and 7 rays respectively; pectoral fins with 13 to 17 rays. Caudal rounded or truncate, occasionally with produced uppermost and lowermost rays.

The lateral line system of *Sphoeroides* is similar to that of *Lagocephalus,* and only variations will be discussed here. The transoccipital branch in *Sphoeroides* extends perpendicularly from the dorsal branches across the back, rather than extending from junctions of the supraocular and dorsum branches. The anterior portion of the ventral segment of the lateral lines is more indistinct in *Sphoeroides* than *Lagocephalus.* The branches on the sides of the mouth are usually present, but the extensions on the belly are lacking. However most species have small branches on the belly, lateral to the anal fins. Indiscrete connections sometimes join these branches to the branches on the dorsum.

Nasal papillae vary from short broad tubes to raised elongate tubes; all have medial and lateral apertures. Prickles and lappets vary with species and are discussed under each species treatment. Coloration of each species is also treated separately.

Ecology and Distribution: *Sphoeroides* is a predominently inshore tropical genus, with species that possess limited mobile capacities. Members of the genus are present along the Atlantic coast of Africa, in the western

Figure 8. Lappets and dermal scale-like development in some species of *Sphoeroides*. Upper: Paired black dorsal lappets (medial to pectoral fin). *Sphoeroides marmoratus* RGMC 127766, 7° 16' S., 12° 49' E. Lower: Tan dorsolateral lappets and scale-like dermal structures. *S. greeleyi* ANSP 105681, Venezuela.

Figure 9. Cheek pigmentation, diagnostic to some species of *Sphoeroides*. Upper: *Sphoeroides dorsalis* TABL Silver Bay 5627, off North Carolina. Sexually dichromatic pigmentation of male. Middle: *S. dorsalis* ANSP 105133, off Venezuela. Sexually dichromatic pigmentation of female. Lower: *S. maculatus* FSU 15478, black pepper-like spots.

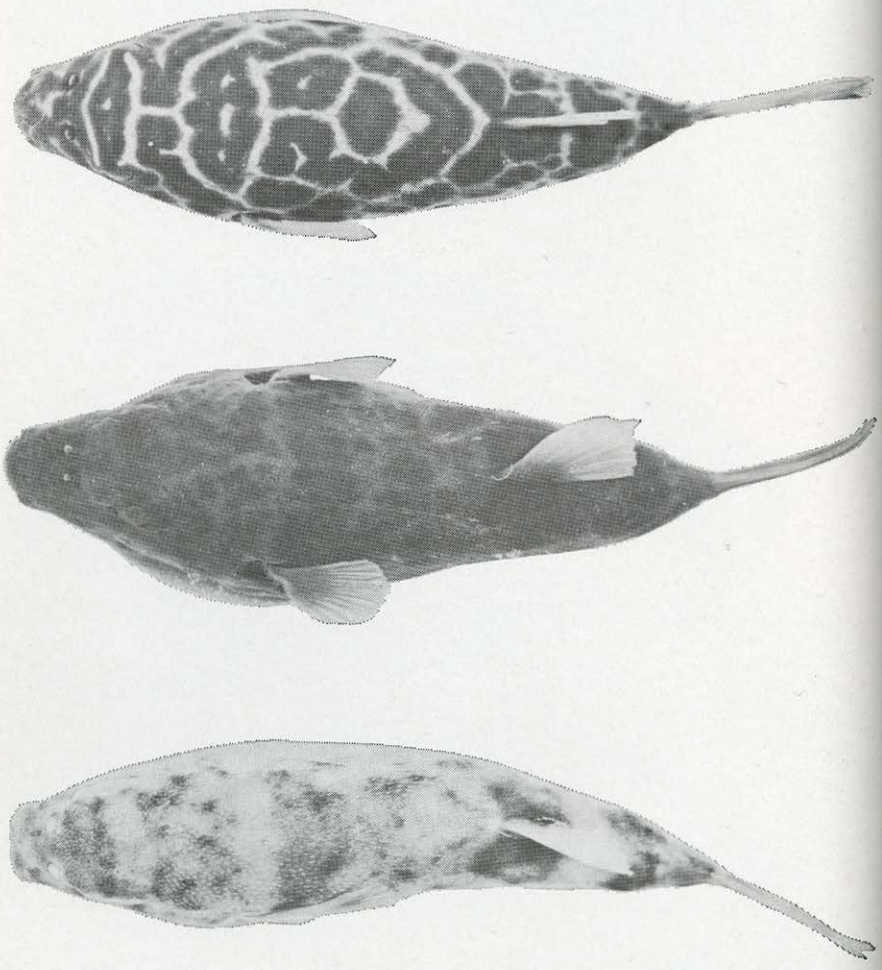

Figure 10. Dorsal pigmentation in some species of *Sphoeroides*. Upper: *S. testudineus* FSU 11928, Jupiter Inlet, Florida. Middle: *S. greeleyi* ANSP 105681, Venezuela. Lower: *S. parvus* FSU 15365, Mobile Bay, Alabama.

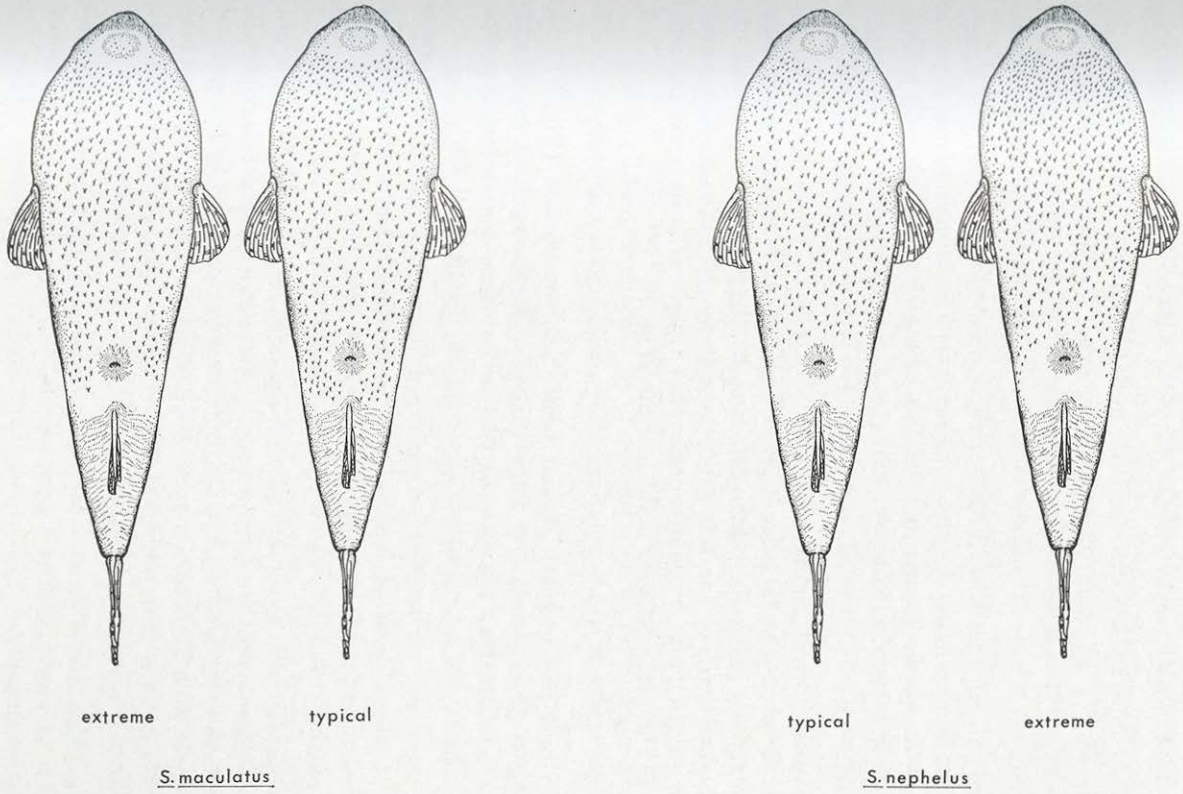

Figure 11. Distribtuion of prickles on the ventral surface of *Sphoeroides maculatus* and *S. nephelus* showing posterior extent in relation to anal opening (from Shipp and Yerger 1969a).

Atlantic and adjacent waters, and along the eastern Pacific coast. One species only, *S. pachygaster,* is circumglobal and occurs in all tropical and temperate seas.

KEY TO SPECIES *SPHOEROIDES* OF THE ATLANTIC OCEAN

A. Body entirely smooth, prickles totally lacking. Interorbit broad, usually 8% or more of standard length. Pigmentation mostly uniform, except usually a few dark spots on the flanks ..... *S. pachygaster* (Müller and Troschel)

AA. Body usually with prickles (prickles often not exposed, but present beneath tiny pores in the integument). Interorbit of moderate to narrow width, usually 8% or less of standard length. If prickles absent, interorbit concave, narrow, 5% or less of standard length. Pigmentation variously mottled ..... B

B. Lappets (small fleshy tabs most easily seen when specimens are immersed in fluid) present on dorsal and/or lateral surfaces; sometimes only a single black pair on the dorsum about one-half the distance between the posterior margins of the orbits and the dorsal fin origin (Fig. 8), and/or scattered light tan lappets concentrated near the posterolateral body margin (Fig. 8) C

BB. Lappets absent ..... H

C. A single pair of black lappets present on the dorsum (Fig. 8). No lappets on posterolateral body surface. Cheeks marbled in subadult and adult males (Fig. 9). From 1 to 5 diffuse dark blotches present on the lateral body surface posterior to the pectoral fin ..... *S. dorsalis* Longley

CC. Black dorsal pair of lappets present or absent, light or tan lappets present on posterolateral portions of body (Fig. 8). Cheeks variously pigmented but not marbled as in Fig. 3 ..... D

D. Lappets present as a black pair on the dorsum and light or tan lappets on posterolateral portions of body. One to three distinct dark blotches beneath eyes. Usually four distinct dark spots form the lower cheek margin, and four to six more such spots on the ventrolateral body angle form a row posterior to the pectoral fin, the more posterior ones less distinct ..... *S. marmoratus* (Lowe)

DD. No black dorsal pair of lappets present. No dark blotches beneath eyes. Lower cheek, and ventrolateral body margin with or without marginal spots ..... E

E. Lower lateral surfaces lacking pigment except for many tiny black flecks or speckles. Least bony interorbit narrow, about 5 or more in snout, pectoral rays usually 14, rarely 13 or 15, (Table 2) ..... *S. yergeri* Shipp

EE. Lower lateral surfaces marked with blotches or spots, not with tiny black flecks or speckles. Least bony interorbit either broad, less than 5 in snout, or if narrow, pectoral rays usually 16 (rarely 15) ..... F

F. Pectoral rays 15 or 16 (Table 2). Lower cheek with three or four vague diagonal blotches, not evident in poorly preserved specimens ..... *S. tyleri* Shipp

FF. Pectoral rays 13 to 15. Lower cheek with a row of four to six very distinct round spots, or with many discrete spots of various shapes, but not with three or four vague diagonal blotches ..... G

G. Lower margin of lateral surface bounded by a regular series of distinct, uniform, rounded spots, four to six anterior and seven to nine posterior to the pectoral fin. Caudal fin with dark, sharply defined proximal and distal bars (Fig. 2) ..... *S. spengleri* (Bloch)

GG. Lower margin of lateral surface with many broken blotches or spots, irregularly placed and shaped. Caudal fin with a poorly defined, vaguely barred pattern ..... *S. greeleyi* Gilbert

H. One or two distinct, transverse, white interorbital bars, the posterior one often connected by a posterior perpendicular extension to a dorsal pattern of coarse white arches and circular markings (Fig. 10). ..... *S. testudineus* Linnaeus

HH. Vague dark interorbital bar. Dorsal pattern variously mottled, but not with coarse white arches and circular markings (Fig. 10) I

I. Several (usually 6-8) distinct, vertically elongate bars posterior to pectoral fins. Dorsal and lateral surfaces in mature specimens (above 70 mm) covered with tiny (to 1 mm) jet black spots (Fig. 9). Prickles on ventral surface extend posteriorly beyond the anus, usually to the anal fin origin (Fig. 11). Pectoral rays 15-17, usually 16 (Table 2) ..... *S. maculatus* (Bloch and Schneider)

II. Lateral markings posterior to pectoral fins varied, but not distinct, vertically elongate bars. No tiny (to 1 mm) jet black spots over dorsal and lateral surfaces, except rarely a few beneath the eye. Prickles on ventral surface, if present, do not extend beyond the anus (see *S. nephelus,* Fig. 11). Pectoral rays 13-17 ..... J

J. Spot at axil of pectoral fin more intense than any other spots on body (as in Fig. 12). Bony interorbit usually concave; least bony width narrow, more than 4 in snout. Adults often marked with discrete white (or green in fresh or live specimens) reticulate, vermiculate or circular markings ..... *S. nephelus* (Goode and Bean)

JJ. Spot at axil of pectoral fin absent, or if present rarely more intense than any other spots on body (Fig. 12). Bony interorbit nearly

flat, least bony width moderate, less than 4 in snout. Adults with diffuse, indiscrete white (or green in fresh or live specimens) markings, or no such markings at all ..... K

K. Pectoral rays 16, rarely 15 or 17 (Table 2). Prickles on dorsum present only in a narrow strip from the nape to the level of the posterior margin of the pectoral fin. Prickles never present on cheeks or lateral surface ..... *S. georgemilleri* Shipp

KK. Pecoral rays 14 or 15 (rarely 13 or 16). Prickles on dorsum extend posteriorly from the nape (or anterior to nape) to dorsal fin origin, and often present on cheeks or on lateral surfaces posterior to pectoral fin L

L. Snout and head extensively covered with prickles, which extend anteriorly on the snout to at least between the nasal papillae ..... *S. parvus* Shipp and Yerger

LL. Prickles present on the head only on the interorbit, and posteriorly to the origin of the dorsal fin, not present anteriorly to between the nasal papillae. Individuals of *S. greeleyi* from some population of the Central American and southern Brazilian coast may rarely lack lappets and key here; see also GG ..... *S. greeleyi* Gilbert

Sphoeroides pachygaster (Müller and Troschel) Blunthead Puffer
(Figs. 13 and 14)

? *Tetraodon laevissimus* Cuvier 1829:368 (as a footnote, Bloch and Schneider erroneously cited as author of species) nomen oblitum, and preoccupied by *T. laevissimus* Bowditch 1825, also nomen oblitum (see *S. marmoratus*).

Tetrodon (*Cheilichthys*) *pachygaster* Müller and Troschel 1848a:677 (original description, Barbados).

? Sténométope laevissimus (Bibron) Duméril 1855:278 (from Bibron's manuscript list of species of Sténométope).

? *Stenometopus laevissimus* (Bibron) Troschel 1856:88 (after Duméril).

Tetrodon (*Liosaccus*) *cutaneous* Günther 1870:287 (description, St. Helena, ? Cape of Good Hope).

Tetrodon (*Liosaccus*) *pachygaster.* Günther 1870:287 (after Müller and Troschel).

Tetrodon cutaneus. Melliss 1875:112 (St. Helena). Cunningham 1910: 118 (St. Helena). Jordan 1923:357 (designates *T. cutaneus* as type-species of *Liosaccus* Günther). Barnard 1927:971 (S. Africa, St. Helena, Azores).

Sphoeroides (also *Sphaeroides, Spheroides*) *pachygaster.* Jordan and Edwards 1886:235 (after Müller and Troschel). Jordan 1886b:605 (West

Figure 12. Axil pigmentation in two species of *Sphoeroides*. Upper: *S. nephelus* FSU 13889, northwest Florida. Lower: *S. parvus* FSU 15365, Mobile Bay, Alabama.

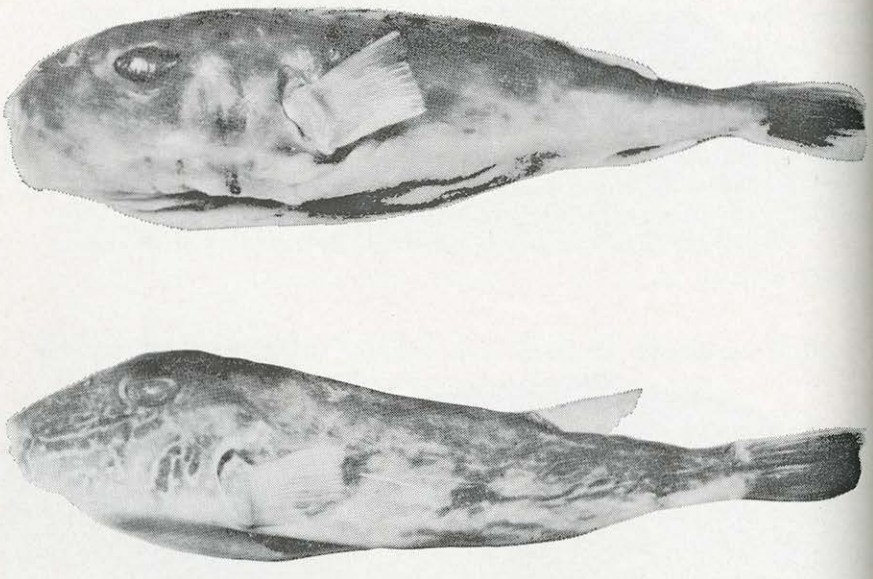

Figure 13. Upper: *Sphoeroides pachygaster* ANSP 105124 (133 mm SL), off Colombia. Lower: *S. dorsalis* TABL Silver Bay 5627 (133 mm SL), off North Carolina.

Indies, after Müller and Troschel). Jordan and Evermann, 1898:1738 (after Müller and Troschel). Reid 1944:216 (description, figure, Virginia). Bullis and Thompson 1965:61 (catch records). Cervigon 1965:68 (Venezuela) and 1966:842 (key, figure, description, Venezuela). Shipp and Yerger 1969b:484 (key, figure, Atlantic Ocean). Bailey et al. 1970:63 (check list, Atlantic).

? *Sphoeroides spengleri* (not of Bloch). Murray and Hjort 1912:411 (figure, Canary Islands).

Liosacus (also *Liosaccus*) *intermedius* Ribeiro 1915:6 of Tetraodontidae section (original description, Brazil), and 1918:66 (synonymy, Brazil). Fowler 1941:183 (Brazil). Ribeiro 1961:6 (type-specimen in Museu Nacional, Rio de Janeiro).

Liosaccus cutaneus. Fowler 1919a:195 (Azores), and 1936:1111 (description, figure, Azores). Cadenat 1950:287 (Senegal). Fowler 1952: 145 (New Jersey). Poll 1959:344 (description, figure, ecology, Africa).

Sphoeroides dubius Bonde 1922:40 (original description, figure, S. Africa).

Spheroides joani Lahille 1921:31 (original description, figure, Argentina). Pozzi and Bordale 1935:178 (after Lahille). Ringuelet and Aramburu 1960:53 (after Lahille).

Cheilichthys pachygaster. Jordan, Evermann, and Clark 1930:499 (check list, Barbados).

Thecapteryx lioderma Fowler 1948:677 (original description, New Jersey).

Sphoeroides also *Sphaeroides, Spheroides*) *cutaneus.* Fraser-Brunner 1943:11 (listed as "principal" species of *Sphaeroides*). Smith 1950:417 (key, figure, Atlantic and Indian Oceans). Briggs 1858:300 (Atlantic Ocean, Gulf of Mexico). Gosline and Brock 1960:299 (key, Hawaii).

? *Liosaccus glaber* (not of Freminville). Le Danois 1959:173 (synonymy, in part), and 1961:468 (refers unidentified mounted holotype of Cuvier to *Liosaccus glaber* Freminville).

Discussion of Synonymy: The first diagnostic description of this species was by Müller and Troschel in 1848. Although no type-specimen of these authors has been located, several characters in the original description are diagnostic: "smooth all over, of a light brown color, with darker spots on back. The space between the eyes is equal to two diameters of the eye . . . The caudal is truncated but the upper and lower points are somewhat elongated." No other known member of the family from the vicinity of Barbados (type-locality) had this combination of characters.

Cuvier (1829:368) had earlier referred to a *Tetraodon laevissimus* of Bloch and Schneider, which had a smooth body. However, Bloch and Schneider (1801) mentioned no species by that name, and it is reasonable

to assume that Cuvier intended to cite Klein's Crayracion laevissimus (1744: 18), which is a pre-Linnaean synonym of *Sphoeroides spengleri.* However, a type-specimen of *Tetraodon laevissimus* of Cuvier is present in the Museum d'Histoire Naturelle, Paris. This specimen is mounted, painted, and unidentifiable even to genus (despite Le Danois' assertion (1959:173, 1961:468) that this specimen is conspecific with her *Liosaccus glaber* (=*S. pachygaster*)). *Tetraodon laevissumus* Cuvier is preoccupied by the *Tetraodon laevissimus* of Bowditch, which is itself unidentifable (see discussion of synonymy of *Sphoeroides marmoratus* for details concerning this name). Except for the Latinized list of species from Bibron's manuscript (Troschel 1856:88), *Tetraodon laevissimus* of Cuvier has not been considered a senior synonym since its first usage in 1829, and should therefore be considered a nomen oblitum.

The list of names from Bibron's manuscript published by Duméril (1855) and Latinized by Troschel (1856) includes Sténométope (or *Stenometopus*) *laevissimus.* Bibron used Cuvier's type of *Tetraodon laevissimus* (see above), so these references are included with question in the synonymy of *S. pachygaster.*

Günther (1870:287) described as new *Tetrodon* (*Liosaccus*) *cutaneus.* He also included *T. pachygaster* in this subgenus which was characterized by species lacking prickles. Since Günther listed no specimens of *T. pachygaster* in the British Museum collection, and since his description of this species was taken exclusively from the original description of Müller and Troschel, it is apparent Günther had never seen *T. pachygaster.* If he had, he probably would have realized that the specimens he used to describe *T. cutaneus* (which I have examined) were conspecific with *S. pachygaster.*

Although Jordan and Edwards (1886:235), Jordan (1886b:605), and Jordan and Evermann (1898:1738) placed *pachygaster* into the genus *Sphoeroides,* their treatment of the species indicates complete reliance on Müller and Troschel's original description. Apparently Reid (1944:216) was the first person since 1898 to recognize correctly *S. pachygaster.*

Murray and Hjort (1912:411) listed a *Sphoeroides spengleri* from south of the Canary Islands. Although no description accompanies this citation, the line drawing of the specimen, and depth of capture (39 m) strongly indicate that the species in hand was *S. pachygaster,* which is thus included with reservation in synonymy of this species.

Ribeiro (1915:6 of Tetraodontidae section) raised the subgenus *Liosaccus* of Günther to generic status, and described *L. intermedius* from Brazil. Although I have not examined the type-specimen, Ribeiro's original description and my examination of Brazilian material leaves no reasonable doubt that *L. intermedius* is a junior synonym of *S. pachygaster.*

Bonde's (1922:40) original description and figure of *Sphoeroides dubius* based on material from 27 fathoms off South Africa require inclu-

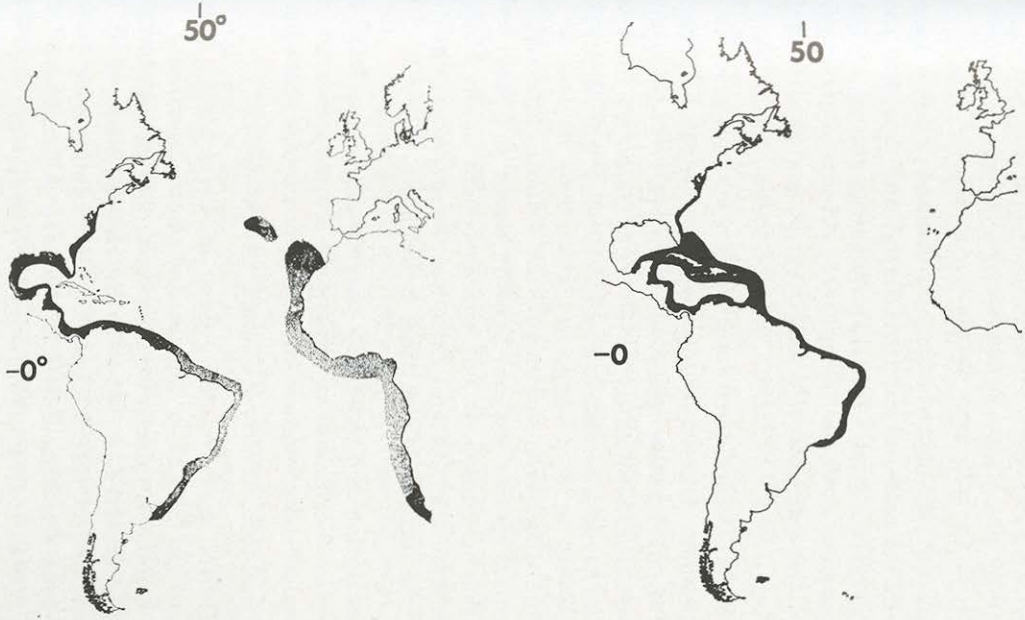

Figure 14. Left: Atlantic distribution of *Sphoeroides pachygaster*. Right: Distribution of *S. testudineus*.

sion of this name as a junior synonym of *S. pachygaster.*

Sphoeroides joani was originally described by Lahille in 1921 (p. 31) from Argentine waters. The excellent description and figure of Lahille, and an opportunity to examine Argentine material identified as *Spheroides joani,* lead me to conclude with no reasonable reservations that *S. joani* is a junior synonym of *S. pachygaster.* Although the type-specimens have been sought, they have not been located and it is possible that they were destroyed by fire at the Museo Argentino de Ciencias Naturales a "few decades ago" (H. P. Castello, pers. comm.).

Fowler (1948:677) created the genus *Thecapteryx* for a specimen of tetraodontid which he collected off New Jersey, and described the species *T. lioderma.* Four years later (1952:145) he synonymized his genus and species under *Liosaccus cutaneus* (Günther) (=*Sphoeroides pachygaster*). I have examined this specimen and find it to be a typical example of *S. pachygaster.*

Le Danois 1959:173 considered most puffers without prickles (including *Tetrodon cutaneus* Günther, *Liosaccus intermedius* Ribeiro, *Spheoroides dubius* Bonde, all junior synonyms of *Sphoeroides pachygaster*) to be *Liosaccus glaber* (Freminville). The *Tetrodon glaber* of Freminville (1813:251, plate IV, fig. 4), based on its written description and figure bears no resemblance to *S. pachygaster* other than its lack of prickles (hardly a reliable diagnostic character). Le Danois incorrectly synonymized these nominal species without prickles under this specific designation. Her decision was based on but two specimens in the Museum National d'Histoire Naturelle. One of these was the aforementioned mounted type of Cuvier; the identity of the other is unknown.

An early description of *Sphoeroides pachygaster* variety *levis* (Borodin 1828:35) from the Caribbean is diagnostic of *Conthigaster rostratus* (Bloch), and undoubtedly is based on specimens of that species.

Material Examined: Thirty-six series, 51 specimens.

Types: MNHN 8340 (1, 208), Cape of Good Hope; holotype of *Tetraodon laevissimus* of Cuvier and *Stenometopus laevissimus* (Bibron) Troschel. (See comments under discussion of synonymy regarding identity of this specimen). BMNH (2, 183-188), St. Helena, syntypes of *Tetrodon cutaneus* Günther. ANSP 71739 (1, 141), off Ventnor, New Jersey, holotype of *Thecapteryx lioderma* Fowler. **Western Atlantic and adjacent waters:** ANSP 71948 (1, 162), off Ventnor, New Jersey. USNM 121952 (1, 160), off Cape Henry, Virginia. TABL, Silver Bay 2190 (1, 136), 34° \$7' N., 76° 06' W. TABL, Silver Bay 1670 (1, 45), 33° 11' N. 77° 08' W. TABL, Silver Bay 5743 (1, 133), 32° 11' N., 79° 08' W. ANSP 99623 (1, 104), Sombrero Key Light, Florida. TABL, Combat 454 (1, 112) 25° 13' N., 80° 10' W. FSBC 3766 (1, 111) 27° 33' N., 84° 22' W. ANSP 97645 (1, 149), 28° 58' N., 84° 44' W. FSBC 3770 (1, 90), 28° 45' N., 85° 04' W. ANSP 97366 (2, 101-120), 29° 02'

N., 85° 46' W. ANSP 97367 (1, 126), 29° 04' N., 85° 49' W. FSBC 550 (1, 138), 23° 36' N., 87° 54' W. USNM 158527 (1, 132), 28° 56' N., 88° 39' W. ANSP 102038 (1, 120), 16° 01' N., 81° 09' W. TABL (Oregon 3567) (1, 196), 14° 11' N., 81° 59' W. ANSP 105124 (1, 133), 12° 09' N., 72° 47' W., off Colombia. MZUSP 7875 (1,160), off the coast of the state of Rio Grande de Sul, Brazil. MACN 1904 (1, 160), 5664 (2, 30-35), off Argentina. **Eastern Atlantic:** ANSP 101322 (1, 74), market at Lagos, Nigeria. RGMC 177764-65 (2, 149-153), 09° 31' 03" N., 16° 23' W. ANSP 106787 (2, 144-184), 05° 08' N., 00° 17' W., Gulf of Guinea. ANSP 106501 (3, 45-150) 05° 06' N., 00° 17' W., Gulf of Guinea. UMML, 21326 (1, 74), 04° 32'-31" N., 05° 07'-13' E. ANSP 103210 (4, 138-165), ANSP 103226 (6, 100-165), ANSP 103230 (1, 45), ANSP 103235 (1, 137) all off Guinea, W. Africa. RGMC 128145 (1, 205), 08° 08' S., 12° 49' E. to07° 55' S., 12° 43' E. **Indian Ocean:** ANSP 108483 (1, 153), 06° 48' S., 39° 51' E. **Pacific Ocean:** USNM 168467 (1, 82) Corregidor, Philippine Islands. ANSP 75576 (1, 185), Hawaiian Islands, Oahu.

Diagnosis: *Sphoeroides pachygaster* is readily identified by its smooth (without prickles) body, broad head, and relatively high dorsal ray count (9) and anal ray count (8 or 9). The body is uniform gray or brown, except for a few dark round lateral and dorsal spots in some specimens.

General Description (Tables 2-4, 6): Head of adults about 2.5 in SL, longer in subadults. Snout short, 1.9 to 2.2 in head, slightly shorter in subadults. Eye large, variable, usually 3 to 4.5 in head. Least bony interorbital flat, broad, 1.8 to 3.0 in snout, about 4.8 in head. Dorsal short, about 1.5 in snout, 3.1 in head, anal usually shorter, about 1.6 in snout 3.3 in head. Dorsal fin origin directly over or slightly anterior to anus, well anterior to anal fin origin. Caudal truncate, but often with uppermost and lowermost rays slightly produced, short, 1.2 to 1.5 in snout, about 3 in head, and shortest in large adults. Pectoral fin moderately short, longest ray about equal to caudal length. Dorsal rays usually 8 or 9 (rarely 7), pectoral rays 14 to 17. Caudal rays 11, with the first upper and two lower rays unbranched.

Pigmentation is a uniform brown or gray on the dorsal and lateral surfaces. This fades on the lower lateral surfaces, and the belly lacks pigment. Specimens from populations of the western Atlantic (and juveniles from the eastern Atlantic) are marked on the pigmented surfaces with dark round or oval spots several mm in diameter; these spots are most prominent laterally. The caudal fin is dusky except the distal tips which are light. The other fins are nearly devoid of pigment.

Lappets and prickles are always absent.

Largest specimen examined had a total length of about 250 mm (about 10 inches), although Müller and Troschel's original description (1848a: 677) is based on specimen(s) of "length fourteen inches".

Geographic Variation: *Sphoeroides pachygaster* is represented by two discrete Atlantic populations. Specimens from the western Atlantic are always spotted, exhibit a high pectoral fin ray count (M=16, n=32), have a large eye (about 4.5 in head) and a very broad bony interorbit (about 2 in snout). Eastern Atlantic populations are uniformly pigmented (except juveniles less than 50 mm SL, which may be spotted), have a moderate pectoral fin ray count (M=14.3, n= 44), an extremely large eye (about 3.5 in head) and a broad bony interorbit (about 2.4 in snout). There is some overlap of all characters. Too few specimens from the Indian and Pacific Oceans were available for study to determine affinities with the Atlantic populations.

Too little is known of the life history and ecology of this species to surmise how effectively isolated (if at all) are the eastern and western Atlantic populations. The great depths at which this species is found and its occurrence near oceanic islands (see ecology and distribution below) may preclude effective isolation. Therefore, until further study material becomes available, I feel it wise to treat these populations as conspecific. Specimens taken from the Indian and Pacific Oceans imply the possibility of one population of worldwide distribution, perhaps partially isolated into mosaically distributed demes. Should specific status of the populations ever be discovered, *S. pachygaster* (Müller and Troschel) would stand for the western Atlantic form, and *S. cutaneus* Günther for the eastern Atlantic species.

Ecology and Distribtuion: *Sphoeroides pachygaster* inhabits relatively deep water, and is more widely distributed than any other known member of the genus. Specimens examined indicate a range in capture depth of from 25 to 480 m. However, very few specimens were taken from less than 100 m.

Stomach contents of individuals from both Atlantic populations indicate that cephalopods, probably squid, comprise the major portion of the diet of this species. Many individuals display small circular cutaneus markings, possibly scars from the discs of caphalopod appendages.

The species is known from New Jersey throughout the western Atlantic and adjacent waters to Argentina, 37° S. (Fig. 14), and from much of the African Atlantic and Indian Ocean coasts (probably Nigeria to Natal). It is also known from St. Helena Island in the Atlantic and from the Philippines and Hawaii in the Pacific.

Sphoeroides dorsalis Longley Marbled Puffer
(Figs. 13 and 16)

Tetrodon (*Spheroides*) *harperi* (not of Nichols) Metzelaar 1919:170 (St. Eustatius).

Sphoeroides (also *Sphaeroides, Spheroides*) *dorsalis* Longley 1934:259 (original description, ecology, Tortugas). Longley and Hildebrand

1940:280 (selection of lectotype, ecology, Tortugas). Longley and Hildebrand 1941 (Tortugas). Schultz 1949:195 (key, description). Hildebrand 1954:320 (ecology, Yucatan, Texas). Hildebrand 1955: 218 (ecology, Yucatan). Briggs 1958:300 (Gulf of Mexico). Bailey et al. 1960:49 (check list, Atlantic). Springer and Woodburn 1960: 89 (ecology, Tampa Bay). Lowe 1962:697 (British Guiana). Bullis and Thompson 1965:61 (catch records). Böhlke and Chaplin 1968: 687 (ecology, Bahamas, North Carolina). Randall 1968:279 (ecology, Caribbean). Shipp and Yerger 1969b:484 (key, figure, Atlantic Ocean). Bailey et al. 1970:63 (check list, Atlantic).

Discussion of Synonymy: *Sphoeroides dorsalis* is one of the most distinctive forms of the genus *Sphoeroides,* and relatively little confusion regarding its identity is found in the literature.

This species was not described until 1934 by Longley, probably due to its rare occurrence in shallow inshore waters. Longley and Hildebrand (1941:280) include two earlier references in synonymy: Metzelaar's (1919: 170) description of *Tetrodon* (*Spheroides*) *harperi* (not of Nichols) from St. Eustatius, and Breder's (1927:79) description of *Spheroides marmoratus* (not of Ranzani) from three locations in the Bahamas.

The former reference is not identifiable to species from Metzelaar's description, but I have examined three specimens identified as *Tetrodon harperi* from Prof. Boeke's St. Eustatius collection (on which Metzelaar's work was based), and they are indeed young specimens of *S. dorsalis.* Although these specimens are not the same individuals and do not fall within the size range given for those examined by Metzelaar, their locality and identification are the same, which strongly indicates this is the species Metzelaar had in hand. This reference has thus been included in the synonymy of *S. dorsalis.*

The latter reference (Breder 1927) includes a description which is evidently of *Sphoeroides nephelus,* a species much more likely to be encountered in the shallow waters of the Bahamas than *S. dorsalis,* and is therefore not included in the synonymy. Subsequent references to *S. dorsalis* are in all probability correct regarding identification because of the distinctive specific characters included in the early descriptions.

Material Examined: Thirty-one series, 69 specimens.

Types: USNM 109179, Tortugas, Florida. Lectotoype of *Sphoeroides harperi* Longley and Hildebrand. USNM 109180 Tortugas, Florida, paralectotype of *Sphoeroides harperi* Longley and Hildebrand. **North America:** USNM 111567 (1, identified only, not measured). TABL, Silver Bay 5627 (1, 133), off North Carolina. ANSP 105614 (1, 133), off Georgia. TABL, Silver Bay 5099 (2, 53-59). TU 13179 (1, 148), off Florida. GCRL 1281 (2, 112-122) off Alabama. GCRL 1280 (1, 135), 2786 (1, 135) off Louisiana. NMFS-G BT 27 W19 (1, 111), off Texas. **Central and South America:** TABL 67-88 (1, 79), 67-90 (7, 62-80), 67-91 (3, 42-67), 67-93 (3, 50-67),

67-94 (6, 57-87), 67-96 (1, 59), 67-97 (8, 46-89), 67-111 (7, 63-117), off eastern Honduras. ANSP 107321 (1, 46), off Panama. ANSP 105123 (1, 118), 105139 (1, 102), off Colombia. ANSP 101830 (1, 115), 105133 (3, 110-126), 107325 (1, 63), off Venezuela. ANSP 103151 (1, 69), 103154 (1, 117), off Surinam. **Caribbean Islands:** ANSP 106727 (1, 89), off Puerto Rico. RMNH 9853 (1, 39), 9860 (3, 28-29), off St. Eustatius Island. ANSP 108490 (3, 75-110), off Windward Islands. ANSP 105185 (2, 104-129), off Trinidad.

Diagnosis: *Sphoeroides dorsalis* is one of the most distinctive members of the genus, easily recognized by the presence of a pair of black lappets on the dorsum, but the absence of other lappets on the posterior dorsal and lateral body surface. In very young juveniles (less than 40 mm SL) the dorsal lappets may be light tan and quite inconspicuous against the dorsal body color. In addition, adult males display a very distinctive pigmentation pattern (Fig. 9). The cheeks are scrawled with light, discrete markings of irregular patterns. This pattern is extremely diffuse or absent in females (Fig. 9).

General Description (Tables 2-4, 6): Head of adults 2.5 to 2.8 in SL, longer in subadults. Snout 1.6 to 2.0 in head, and relatively longer in adults; eye about 4 in head. Least bony interorbit narrow, about 6 in snout length (from 4 in snout length in very young individuals to 8 in large adults), and about 10 or 11 in head length. Dorsal about 1.3 in snout, about 2.4 in head; anal about 1.6 in snout, about 2.9 in head. Dorsal origin opposite anus, slightly anterior to anal fin origin. Caudal slightly concave, medial rays slightly shorter than snout. Pectoral length 1.2 to 1.7 in snout, about 2.7 in head. Dorsal rays 8, anal rays 7, pectoral rays 16, occasionally 15, rarely 17, with a distinct rudimentary ray (not included in count) originating from the upper fin sheath, and about 2/5 to 2/3 the length of the first full ray. Caudal rays 11, with the first upper and two lower rays unbranched.

Pigmentation is restricted to dorsolateral surfaces. Basal pigmentation is uniform gray or brown, with a few poorly defined darker bars or blotches on the dorsum. A vague, diffuse bar extends over the interorbital region, and one or two diffuse blotches are found posterior to the orbits. Usually a small spot or weak bar is evident just posterior to the hind margin of the depressed dorsal fin. Laterally, one to five diffuse spots border the pigmented surface posterior to the pectoral fins, and two or three diagonally elongate diffuse spots mark the ventral cheek border. Sexual dichromatism is evident; in adult and subadult males a distinct but irregular pattern of scrawl-like markings is often found on the cheek (Fig. 9). Sometimes this pattern may extend posteriorly to the caudal peduncle along the ventrolateral body angle. Some females exhibit very faint suggestions of this scrawl-like pattern, but most lack it entirely. The caudal fin is pigmented with a more or less distinct bar at its base and another at its posterior margin. The dorsal and anal fins are

sometimes lightly pigmented, most often near their posterior margins.

A single pair of black lappets is present on the dorsum about half the distance from the posterior margin of the orbits to the dorsal fin origin (as in Fig. 8). Rarely one of the pair may be absent. These lappets may be tan or light gray in small juveniles. Lappets are absent elsewhere on the body.

Prickles are always present on the dorsum from the anterior part of the snout posteriorly to the dorsal lappets or beyond, sometimes to near the dorsal fin origin. Prickles are often lacking on the cheeks and belly, but when present ventrally, prickles terminate well anterior to the anus, usually near the level of the pectoral fin margin. These are much more widely spaced near the center of belly than near its margins, often leaving large areas of the belly without prickles.

Sphoeroides dorsalis is a moderate-sized puffer which may reach about 175 mm (about 7 inches) in total length.

Geographic Variation: No significant geographic variation was detected in pigmentation pattern or morphometric characters. Many individuals from South American waters lacked prickles on the belly, whereas individuals without prickles were uncommon in other localities.

Ecology and Distribution: *Sphoeroides dorsalis* is most frequently taken in trawl samples from moderate depths, 10 to 50 fathoms. However, Böhlke and Chaplin (1968:687) mentioned a large series of young dipnetted under a light at night in the Bahamas. Also, the collections of Dr. Boeke from St. Eustatius include very small specimens from shallow depths. However, I have seen no adults from less than 10 fathoms. This may indicate that young juveniles and adults prefer different habitats. Because most puffers less than 30 mm SL are rather nondescript in their pigmentation patterns, it is possible that young *S. dorsalis* have from time to time appeared in juvenile series of other species and were not recognized.

Randall (1968:279) noted a preference for clear water by this species; however, as it is known from muddy waters off Mississippi and Louisiana, turbid water apparently is no ecological barrier.

Nothing is known of its spawning habits. Examination of gonads indicates that sexual maturity is attained by specimens 100 mm SL, and some specimens as small as 50 mm SL show incipient gonadal development. The sexually dichromic pigmentation pattern discussed above develops synchronously with maturation of the testes.

Sphoeroides dorsalis occurs from North Carolina southward throughout the Caribbean and Gulf of Mexico to Surinam (Fig. 16). Although it has never been recorded as abundant, it is frequently taken in shrimp trawls and can hardly be considered as a rare species.

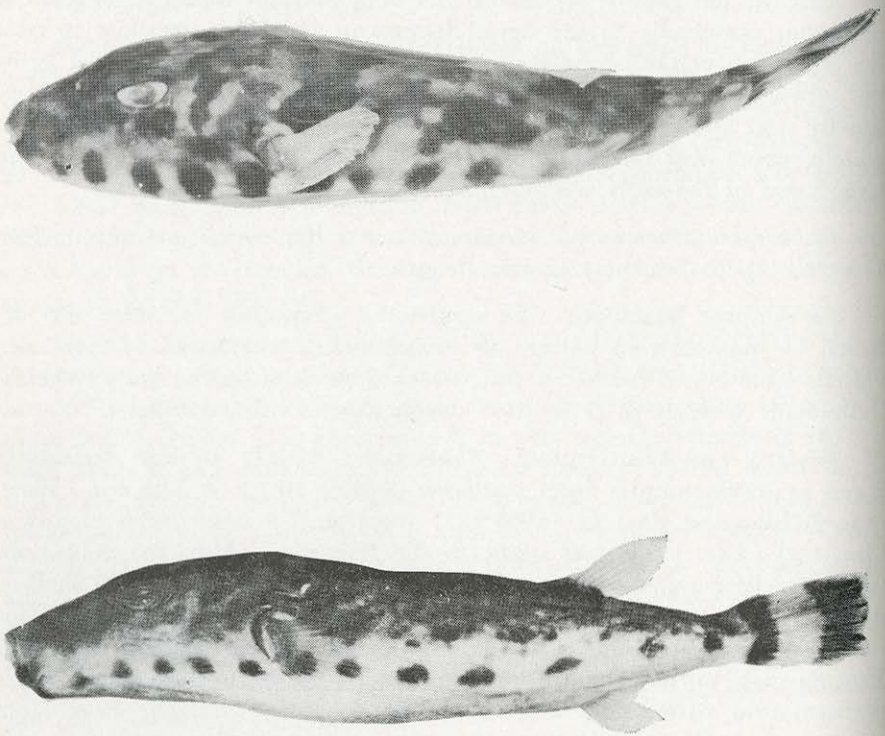

Figure 15. Upper: *Sphoeroides marmoratus* RGMC 127766 (133 mm SL), 7° 16' S., 12° 47' E., of Angola. Lower: *S. spengleri* ANSP 104557 (119 mm SL), Colombia.

Sphoeroides marmoratus (Lowe) Guinean Puffer

(Figs. 15 and 16)

? *Tetraodon laevissimus* Bowditch 1825:233 (original description, undetermined species of tetraodontid, Madeira), a nomen oblitum.

Tetrodon marmoratus Lowe 1839:193 (original description, Madeira). Valenciennes (in Webb and Berthelot) 1843:94 (Teneriffe, Madeira). after Lowe). Roule 1919:63 (Boa Vista, Cape Verde Islands, considered by Roule as possibly a subspecies of *Tetrodon spengleri* Bloch (=*Sphoeroides spengleri*)).

Sténométope marmoratus (Bibron) Deméril 1855:278 (included in Bibron's manuscript list of species of Sténométope).

Stenometopus marmoratus (Bibron) Troschel 1856:88 (based on type of *T. marmoratus* Valenciennes).

Tetrodon spengleri (not of Bloch). Günther 1870:284 (description, Madeira, Lanzarote, Cape Verde Islands, West Africa, in part). Rochebrune 1882:178 (Guet n' Dar Dakar, Goree). Osorio 1890:59 (Toulson and Ferreira Sampaio, Angola).

? *Tetraodon bronkenii* Poggi 1881:35 (original description, Canary Islands).

Sphoeroides spengleri (not of Bloch). Jordan and Gunn 1898:344, Canary Islands). Fowler 1919a:267 (Gabun, French Congo) and 287 (diagnostic description, Loanda, Angola) and 1936:1107 (synonymy, Madeira, Azores, and Gambia). Noronha and Sarmento 1948:126 (Madeira). Maul 1949:30 (Madeira). Cadenat 1950:285 (Senegal) Nunes 1953:220 (Madeira). Le Danois 1959:198-200 (systematics; in part, includes in synonymy many western Atlantic and eastern Pacific forms which are valid species). Poll 1959:345, 346 (diagnostic figure and description, many Angola localities south to Bay of Tigers). Le Danois 1961:470 (lists Valenciennes' type in Museum National d'Histoire Naturelle).

Discussion of Synonymy: *Sphoeroides marmoratus* is an eastern Atlantic geminate of the western Atlantic *S. spengleri* (Bloch). On cursory examination, the two forms appear conspecific. This has led to a nearly unanimous inclusion of records of *S. marmoratus* from African and adjacent waters under the specific name *spengleri.* However, recent examination of sufficient material by George Miller (of the Tropical Atlantic Biological Laboratory) and myself has revealed important distinctions between the two forms. A literature search by Miller and examination of types by both of us has led to the conclusion that *Tetrodon marmoratus* Lowe (1839:193) should be considered as the correct name for this distinct eastern Atlantic species.

An earlier name, *Tetrodon laevissimus,* was presented by Bowditch (1825:233) along with an extremely impressionistic figure and description, unidentifiable to species. The type locality, Cape Verde, and fin

ray counts (P. 13; A. 7; D. 7; C. 7) indicate that the name may have been based on specimens of *Sphoeroides marmoratus.* In any case, the name has not been used as a senior synonym since its introduction. Therefore, *Tetrodon laevissimus* Bowditch should be suppressed as a nomen oblitum, and is included under *S. mormoratus* as a questionable synonym.

It has been necessary to establish the first usage of *Tetrodon marmoratus,* because the name was published independently three times and applied to two species within five years.

According to Sherborn (1927:3899) the *Tetrodon marmoratus* of Lowe appeared first in June, 1839 in the 1841 volume of Transactions of the Zoological Society of London. In 1840, Ranzani published a description of *Tetraodon marmoratus* from Brazilian waters. The description, accompanying figure, and locality leave no doubt as to the identity of Ranzani's species as *Sphoeroides spengleri* (Bloch), and it is so considered as a junior synonym (as well as a junior homonym of *T. marmoratus* Lowe). One year earlier Alessandrini (1839:433) had published a list of species to be included in Ranzani's work, but this usage must be considered as a nomen nudum as it is without description and clearly does not fulfill the requirements of articles 12 and 16 of the International Code of Zoological Nomenclature.

Valenciennes (1843), in Webb and Berthelot's "Histoire Naturelle des Iles Canaries", published a description of *Tetrodon marmoratus* from Teneriffe, Madeira. Although Webb and Berthelot's work was published from 1836 to 1944, volume two, second part, "Ichthyologie des Canaries ou Histoire Naturelle" in which the above cited description occurred, appeared in 1843. Therefore, Lowe's authorship should be accepted over Valenciennes' for this species. In addition, Valenciennes' figure of *T. marmoratus* refers to Lowe. Le Danois (1959:198) is incorrect in attributing 1836 to Valenciennes' work, and 1841 to Lowe's description.

The *Tetraodon marmoratus* of Ranzani has been applied to several species of *Sphoeroides* in the western Atlantic, including *S. nephelus, S. parvus, S. greeleyi,* and *S. tyleri.* Its usage with each of these forms is treated under discussion of synonymy for each species.

Material Examined: Nine series, 13 specimens.

Types: BMNH (1, 123), Madeira, holotype of *Tetrodon marmoratus* Lowe. MNHN 8343 (1, 136), Teneriffe, Canary Islands, mounted specimen, holotype of *Tetrodon marmoratus* Valenciennes and *Stenometopus marmoratus* (Bibron) Troschel. MNHN 8342 (1, 135), Canary Islands, from Webb and Berthelot collection probably used as a paratype (in modern sense) of *Tetrodon marmoratus* Valenciennes. **Madeira:** BMNH (1, 141). BMNH (1, 117, Funchal market. **Africa:** ANSP 106505 (3, 89-103), 106739 (2, 91-100), Gulf of Guinea. MRAC 127770-127771 (2, 47-66), Congo. MRAC 127766 (1, 113), Angola.

Diagnosis: *Sphoeroides marmoratus* is easily identified as it is the only Atlantic species to possess both a black pair of lappets similar to those of *S. dorsalis* as well as tan or flesh-colored lappets along the posterolateral portions of the body. In addition, one to three black spots occur beneath each eye.

This is the only shallow water member of the genus from eastern Atlantic waters. *Sphoeroides pachygaster,* the other eastern Atlantic member of the genus is restricted to relatively deep water (more than 12 fathoms). *S. marmoratus* is easily distinguished from other sympatric tetraodontids by the simple papillae, each with a medial and lateral perforation (an open papillae with two lateral and one posterior flap is present in *Ephippion guttifer*) or by the low dorsal ray count of 8 as opposed to 12 to 15 rays in the species of *Lagocephalus.*

General Description (Tables 2-4, 6): Head of adults 2.5 to 3 in SL. Snout 1.6 to 2.0 in head, the snout relatively shorter in subadults; eye moderate, 4 to 6 in head. Least bony interorbit flat to slightly concave, moderate to narrow, width 4 to 5.5 in snout length, about 8.5 in head. Dorsal and anal of near equal length, about 1.3 in snout, about 2.2 in head. Dorsal origin opposite or slightly posterior of anus, just anterior to anal fin origin. Caudal slightly rounded to nearly truncate, equal or barely longer than snout. Pectoral moderately short, longest ray about 1.4 in snout, 2.5 in head. Dorsal rays 8, anal rays 7, pectoral rays 13-15, with an indistinct rudimentary ray (not included in count) originating from the upper fin sheath, and about 1/5 to 1/8 the length of the first full ray. Caudal rays 11, with the first (and rarely second) upper and two lower rays unbranched.

Pigmentation is restricted to dorsolateral surfaces. Basal pigmentation is uniform tan, but much of the dorsal and upper lateral surfaces are marked with irregular darker and lighter blotchy streaks or bars (Fig. 8). Perhaps the most distinctive of these is a pair of dark wavy postocular bars, each of which originates just anterior to the gill opening and extends dorsally to near the middle of the nape, where the two almost join. Another broader, but more diffuse dark V-shaped bar extends across the dorsum between axils of the pectoral fins, the angle of the V directed posteriorly. Pigmentation of this bar is often so dissipated on the middle of the back that the appearance of a pair of bars results. A vague diffuse interorbital bar is also present. Beneath each eye is a distinct black or brown blotch, sometimes disjoined into two or three small blotches. The lower cheek is bounded by a series of four or five discrete spots of equal intensity with the subocular spots. This cheek series continues posterior to the pectoral fin, but the spots begin to lose intensity about the level of the dorsal fin origin, with the posteriormost spots on the caudal peduncle indiscrete and diffuse. At its base and distal margin, the caudal fin displays vague bars. The fins are nearly devoid of pigment.

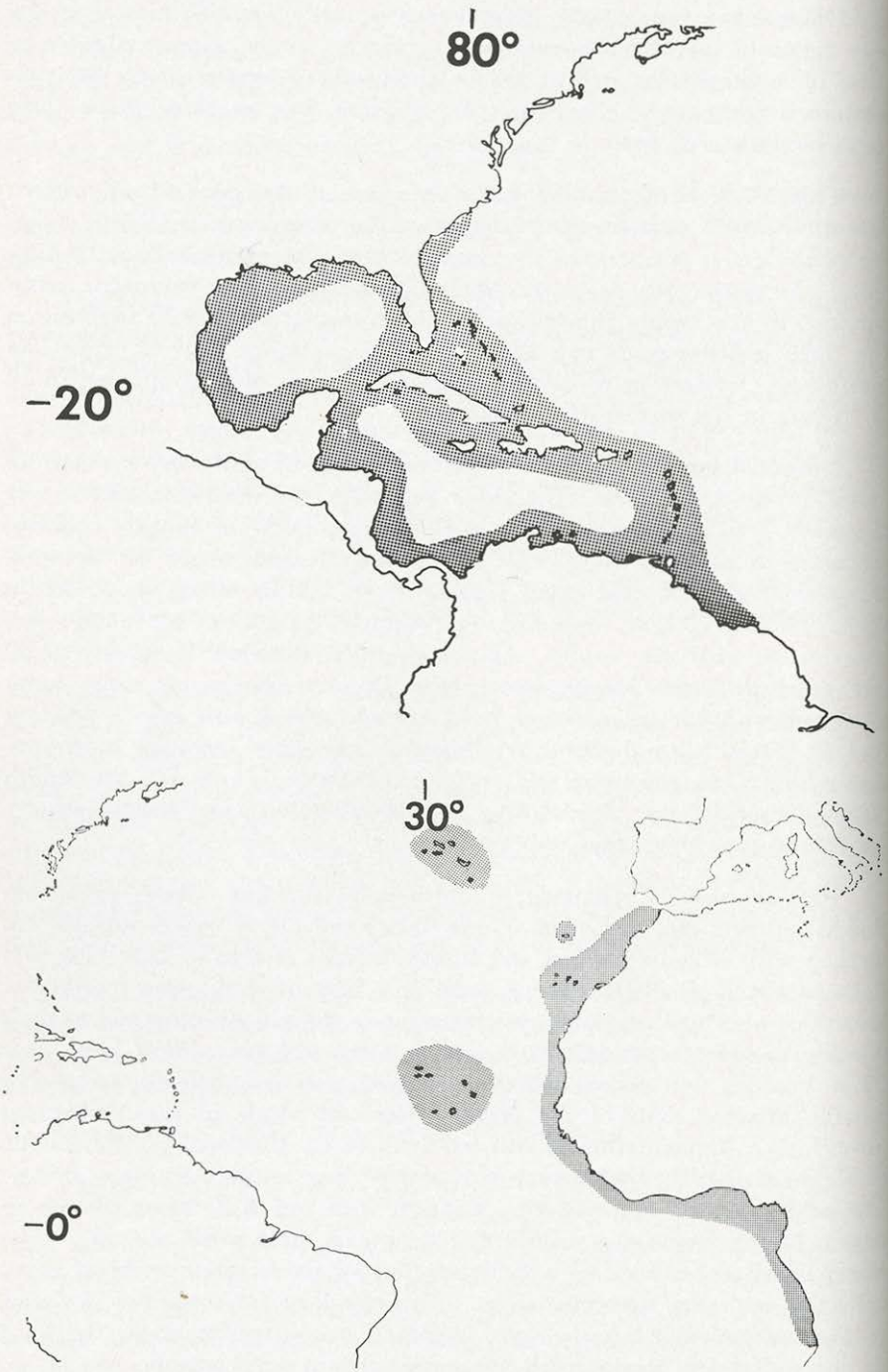

Figure 16. Upper: Distribution of *Sphoeroides dorsalis*. Lower: Distribution of *S. marmoratus*.

Pigmentation in this species is extremely similar to that exhibited by its western Atlantic geminate *S. spengleri.* Chief differences are the presence of subocular spots in *S. marmoratus,* as well as its more marbled contiguous dorsal pattern, somewhat replaced in *S. spengleri* by clusters of spots or a more uniformly solid dorsum. In addition, caudal bars are usually much more distinct in *S. spengleri. S. spengleri* lacks black dorsal lappets (see below). Fowler (1919a:287) noted some of these differences, but considered the populations conspecific.

A single pair of black lappets is present on the dorsum about half the distance from the posterior margin of the orbits to the dorsal fin origin (Fig. 8). Along the lower lateral surfaces posterior to the pectoral fins are several small (1-3 mm) tan or flesh-colored lappets, most concentrated near the ventrolateral body angle. These lappets often are obscure, but can be located most easily while specimens are immersed in fluid.

Prickles may be absent on the dorsum, but if present they extend from the level of the nasal papillae or the nape posteriorly to near the dorsal fin origin. Ventrally, prickles are present from chin to anus. Cheeks and sides usually lack prickles, but occasionally a narrow strip persists along the lower cheek margins.

The largest specimen examined had a total length of 170 mm (about 7 inches).

Geographic Variation: Due to the small number of series available, little significant geographic variation can be discerned. Madeiran specimens lacked prickles on the dorsum, while those from the mainland had prickles. In addition, pectoral ray counts increased in more southerly (colder water) populations. More specimens are needed to verify these observations.

Ecology and Distribution: Little is known of the ecology of *S. marmoratus.* Maul (1949:30) reported the species as common throughout the year along Madeiran coasts. Roule (1919:63) reported specimens from depths of 91 m in the Cape Verde Islands. However, Poll (1959: 345-346) has taken specimens from several bays as well as stations several miles offshore from Angola in the Atlantic. Possibly *S. marmoratus* occupies many niches open to tetraodontids along the eastern Atlantic, as few other species are present there.

Sphoeroides marmoratus ranges along the African Atlantic coast and nearby islands from Madeira to southwestern Angola (Fig. 16). Noronha and Sarmento (1948:126) noted its absence from Portugal, while Mary-Louise Penrith, Windhock, S. W. Africa (pers. comm.) doubts its presence along Southwest African shores.

Sphoeroides yergeri Shipp Speckled Puffer
(Figs. 17 and 18)

Sphoeroides yergeri Shipp 1972: 129 (original description, ecology, dis-

tribution).

Discussion of Synonymy: *Sphoeroides yergeri* apparently has never been identified as any other species. The distinctive pigmentation pattern (see below) would be difficult to confuse with any described form.

Material Examined: Thirteen series, 84 specimens.

Holotype: USNM 206479. An adult female, 64.0 mm SL, collected in a shrimp trawl, 15° 49.5' N., 83° 44' W., off Honduras, in 17 fathoms, by George C. Miller, 7 April 1967.

Paratypes: (all from Central and northwestern South America). TABL 67-89 (8, 57-79), 67-90 (3, 62-78), 67-162 (2, 63-65), 67-167 (7, 60-75), off British Honduras. UMML 23787 (1, 52), off Panama. UMML 30315 (41, 19-40), 30316 (1, 24), 30317 (1, 32), 30318 (4, 24-25), 30319 (3, 22-37), 30320 (11, 30-40), and TABL, Oregon Sta. 4877 (1, 42), off Colombia.

Diagnosis: *Sphoeroides yergeri* is easily recognized by the presence of numerous fine speckles along an unpigmented lower lateral surface. This speckled area extends from the chin to the caudal peduncle, and is bounded below by the ventrolateral body angle, and dorsally by the upper edge of the gill opening. In addition, numerous large white lappets are present on the flanks.

General Description (Tables 2-4, 7): Head of adults 2.6 to 2.9 in SL, slightly longer in subadults. Snout 1.8 to 2.2 in head, and relatively longer in adults. Eye moderate, 3.5 to 5 in head. Least bony interobit concave, narrow, about 5 to 7 in snout with no apparent variance with age, about 12 in head. Dorsal about 1.1 in snout, about 2.2 in head; anal about 1.4 in snout, about 2.8 in head. Dorsal origin opposite anus, slightly anterior of anal origin. Caudal truncate or slightly rounded, with exposed length of medial rays about 0.7 of snout length. Pectoral fins moderate, longest ray 1.2 to 1.4 in snout, about 2.6 in head. Dorsal rays 8, anal rays 7, pectoral rays 13 to 15, usually 14. Caudal rays 11, with the first upper and two lower rays unbranched.

Basil pigmentation, concentrated on the dorsum and upper lateral surfaces, is a uniform gray or brown. Few descriptive patterns are present on the dorsum. A vague, diffuse bar covers the interorbital region, and the remainder of the dorsum displays only a few scattered specks and small blotches. The most distinctive pigment pattern is along the lower lateral surface, where basal pigmentation is lacking, but many tiny (less than 1 mm) black or dark specks extend from chin to caudal peduncle. The chin itself is usually bordered on either side by a narrow ventrad extension of dorsal pigmentation which results in a beard-like appearance. The caudal fin displays a weakly defined bar at its base and another at the distal margin. Other fins have little or no pigmentation.

Conspicuous lappets are present along the posterolateral surfaces pos-

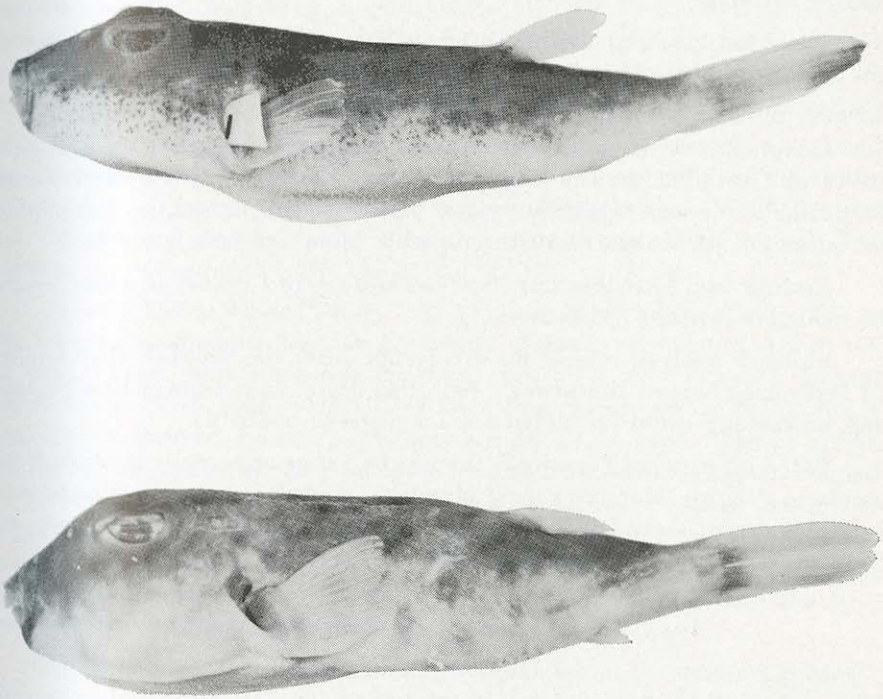

Figure 17. Upper: *Sphoeroides yergeri* TABL 67-89 (79 mm SL), paratype, off Honduras. Lower: *S. tyleri* ANSP 117311 (91 mm SL), holotype, off Surinam.

terior to the pectoral, and are especially prevalent near the ventrolateral body angle. These fleshy tabs are white or light colored, and in adults most exceed 2 mm.

Prickles are present on the dorsum from the snout to near the dorsal fin origin, and on the ventral surface anterior to the anus. Prickles may also cover portions of the cheeks and flanks, or may be absent from the lateral surfaces.

Based on material examined, *S. yergeri* is a small species, with a maximum total length of about 100 mm (about 4 inches). This small species attains sexual maturity at about 50 mm SL.

Geographic Variation: *Sphoeroides yergeri* is limited to about 1000 miles of Central American coastline. Such restricted distribution would be unlikely to reveal significant clinal variation, and in fact, no geographic variation of any nature is distinguishable from available material.

Ecology and Distribution: *Sphoeroides yergeri* occurs in clear waters of moderate depth, 10-35 fathoms.

Stomach analysis reveals no divergence from the shellfish diet typical of other members of the genus. No other significant information regarding its ecology could be inferred from material available.

Based on material examined, the species range apparently extends from southern British Honduras to Colombia; however, no collections were available from likely habitats along Nicaragua, Costa Rica, and most of Panama, so its presence there can only be inferred (Fig. 18).

Sphoeroides tyleri Shipp Bearded Puffer
(Figs. 17 and 18)

Sphoeroides marmoratus (not of Ranzani) Lowe 1962:697 (British Guiana).

Sphoeroides tyleri Shipp 1972:131 (original description, figure, ecology, distribution).

Discussion of Synonymy: *Sphoeroides tyleri* occurs in moderate depths along the northeastern coasts of South America where the ichthyofauna is poorly known. Evidently no descriptions of this species other than the above have been made. I have examined material in the British Museum referred to in the Lowe citation above and find it to be this species.

Material Examined: Twenty-one series, 37 specimens, all from South America.

Holotype: ANSP 117311 (1, 91), adult male, 06° 50' N., 54° 04' W., off Surinam in 28 fathoms. **Paratypes:** UMML (1, 43), 30322 (3, 39-48), 30323 (2, 26-31), 30324 (5, 38-45), 30325 (1, 30), 30326 (5, 27-41), and ANSP 101832 (1, 91), off Colombia. EIMM-F. C. 1396 (1, 38), and ANSP 117317 (1, 87), off Venezuela. EIMM-F. C. 1554, Gulf of Paria,

Venezuela. UPR 1821 (1, 62), Trinidad. BMNH (1, 87), off British Guiana. EIMM-F. C. 2155 (1, 77), 2185 (2, 47-55), and RMNH (1, 81), off Surinam. ANSP 101359 (1, 89), off French Guiana. ANSP 101361 (3, 70-84), off Sao Luis, Brazil. ANSP 100131 (2, 84-85), off Parnaiba, Brazil.

Absolute identification of the following specimens was precluded, and they are not designated as paratypes: MZUSP 7693, 7694 (2, 33-37), off Aracaju, Sergipi, Brazil, small size and undeveloped pigmentation pattern, and MZUSP 3197 (2, 86-96), Bahia, Brazil, poor preservation.

Diagnosis: *Sphoeroides tyleri* possesses an indistinct pigment pattern of diffuse spots and blotches. The chin of adults is heavily pigmented on either side, and thus appears to bear a beard absent only in the center of the chin. The bony interorbit is narrow and concave. White lappets are concentrated on the flanks near the ventrolateral body angle. The pectoral ray count is usually 15 or 16.

General Description (Tables 2-4, 7): Head of adults 2.4 to 2.8 in SL, longer in subadults. Snout 1.7 to 2.1 in head. Eye large, 3.5 to 4.5 in head. Least bony interorbit concave, narrow, 4 to 6 in snout length, about 10 or 11 in head. Dorsal 1.1 or 1.2 in snout, about 2.4 in head; anal a little shorter, 1.3 or 1.4 in snout, about 2.7 in head. Dorsal origin nearly opposite anus, slightly anterior to anal fin origin. Caudal rounded to truncate, often with the upper rays slightly longer than the lower, length 0.8 to 1.0 in snout, about 1.8 in head. Pectoral moderately long, longest ray about 1.1 in snout, 2.2 to 2.4 in head. Dorsal rays 8, anal rays 7, pectoral rays 15 or 16 (rarely 14). Caudal rays 11, with the first upper and two lower rays unbranched.

Pigmentation is restricted to dorsolateral surfaces. Basal pigmentation is uniform tan which is darkest dorsally and fades laterally well above the ventrolateral body angle. A dark interorbital bar is present. The dorsum is covered with scattered dark spots, a pair of which is always present medial to the pectoral fins. In well marked specimens, light transverse areas may give the dorsum a vague saddled appearance. An indistinct row of round or slightly elongate blotches borders the ventral margin of the flanks. The cheeks may exhibit irregular horizontal bars which extend forward from the pigmented area beneath the eye to the lower cheek border, or these may be so vague as to leave the lower cheek nearly without pigment. The caudal fin is pigmented with a more or less distinct bar at its base and another at its posterior margin. The other fins are nearly devoid of pigment.

Light fleshy tabs or lappets are present on the posterolateral surfaces, mostly concentrated along the dorsolateral body angle. Two or three of these lappets are usually present on the flanks at or near the level of the posterior margin of the depressed pectoral fin.

Prickles are present over most body surfaces anterior to dorsal and

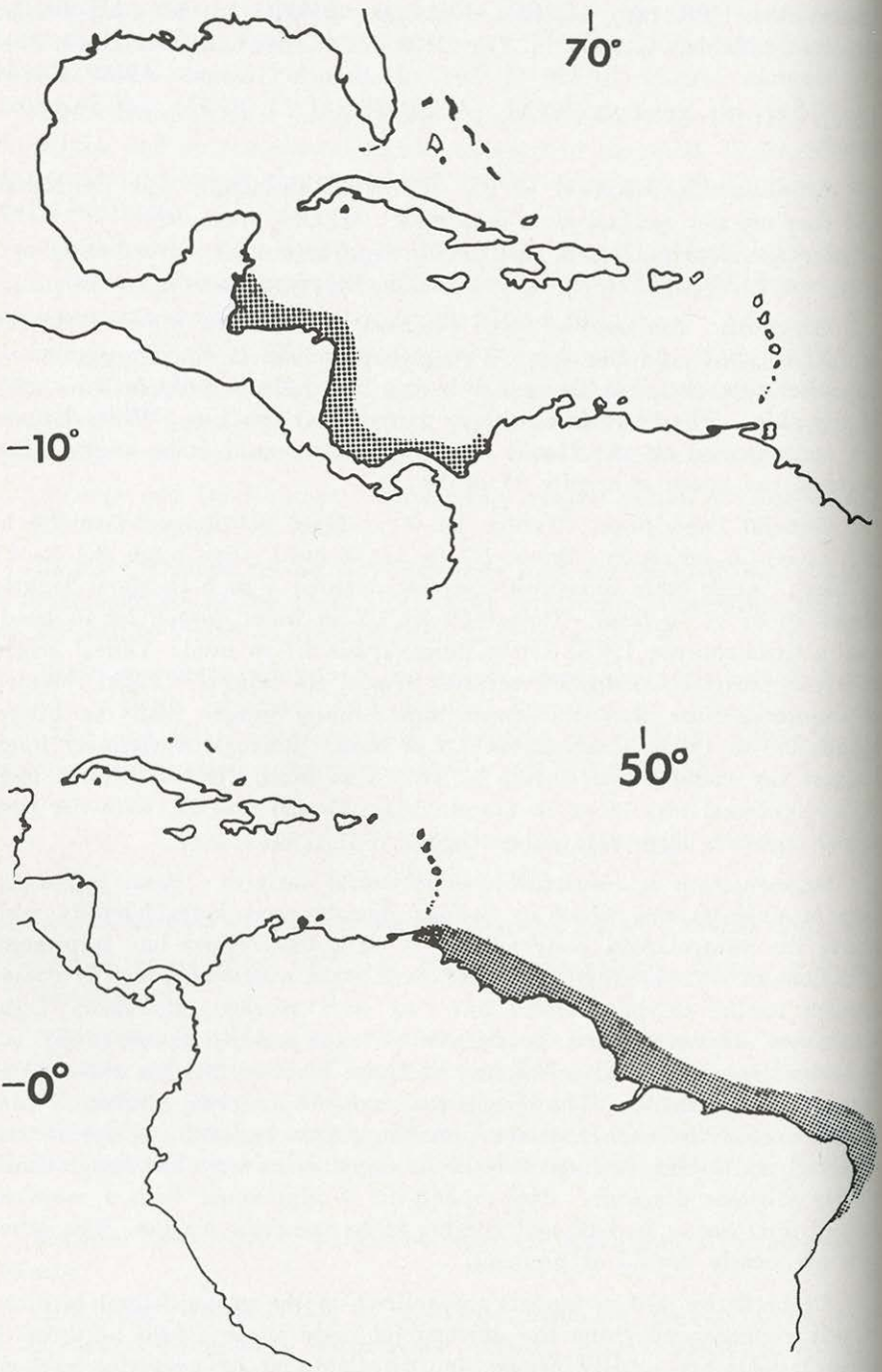

Figure 18. Upper: Distribtuion of *Sphoeroides yergeri*. Lower: Distribution of *S. tyleri*.

anal fins. Sometimes the anterior portion of the snout, upper cheek, or flanks posterior to the pectorals may be partially devoid of prickles. However, in this species prickles are often unexposed and may lie concealed beneath cutaneous pores.

The entire body is covered with small, slightly imbricate dermal structures which are fleshy, and appear similar to squamation of other groups of fishes (Fig. 8). These structures are most easily seen under low magnification on specimens with excess surface fluid removed.

Sphoeroides tyleri is a small puffer. The largest specimen examined was approximately 120 mm (about 5 inches) total length.

Geographic Variation: Some clinal variation of interorbital width appears in this species. Specimens from western populations (Colombia, Venezuela) usually have a narrowed interorbit, contained about 5.5 times in snout length, while in eastern populations (Guianas, Surinam, Brazil) the interorbit is moderate, contained about 4.5 times in snout. Limited material indicates the transition to be gradual. In addition, western populations display more intensive, discrete pigmentation, with the exception of the chin markings which are more distinctive in eastern populations.

Ecology and Distribution: *Sphoeroides tyleri* is most frequently captured in water from 5 to 40 fathoms deep, and where collection data are available, preference for sponge, sand, and shell bottom is indicated. Lowe (1962:697) reported that this species was taken with *S. dorsalis* off British Guiana. Stomach contents included shelled invertebrates, especially echinoderms, and small, whole gastopods.

Sexual maturity is attained between 50 and 80 mm SL.

Sphoeroides tyleri ranges from Colombia to east-central Brazil (Salvador), (Fig. 18). No specimens were taken from Caribbean islands (except continental islands, i.e. Trinidad), probably due to ecological replacement by the very similar *S. nephelus.*

Sphoeroides spengleri (Bloch) Bandtail Puffer

(Figs. 15 and 19)

Tetraodon (also *Tetrodon*) *spengleri* Bloch 1785:144 (original description, figure). (Linnaeus) Gmelin 1788:1446 (after Bloch). Lacépède 1798:476, 510 (after Bloch). Bloch and Schneider 1801:504 (description, after Bloch and Gmelin, incorrect locality - Tranquebarium (Indo-Pacific)). Shaw 1804:445 (after Bloch (West ?) Indian Seas). Cuvier 1829:369 (footnote, brief description, after Bloch and Seba). Castelnau 1855:98 (Bahia, Brazil). Günther 1870:284 (description, Santa Cruz, Cuba, in part). Cope 1871:478 (species spelling: *spenglerii,* description, from St. Martins, Tortugas, and New Providence). Jordan and Gilbert 1883c:861 (description, North America).

Garman 1896:93 (Bahamas). Roule 1919:63 (after Bloch, similarities with African cognate *S. marmoratus* noted). Beebe and Tee-Van 1928:265 (Haiti). Nichols 1930:346-347 (Porto Rico). Nichols and Breder 1943:140 (Woods Hole, Massachusetts).

Tetrodon (*Sphoeroides*) *spengleri* Metzelaar 1919:169 (description, St. Eustatius, West Indies, and Curacao).

Le Tetrodon Plumieri Lacépède 1798:476, 504 (poor figure, original description, vernacular). Bloch and Schneider 1801:509 (description, American islands). Cuvier 1816:338 (footnote, placed in synonymy of *T. spengleri* Bloch).

Le Sphéroide tubercule Lacépède 1798:23 (based on a front view of a figure of *T. tuberculatus* (=*T. spengleri* Bloch) in Plumier's manuscript, erroneously considered generically distinct, see below and discussion of synonymy of the genus *Sphoeroides*).

Cirrhisomus Sprengleri Swainson 1838:328 (type-species of *Cirrhisomus; Sprengleri* is an obvious misspelling of *spengleri* Bloch; species referred to Bloch's description). Swain 1882:282 (synonymizes *Cirrhisomus* with *Tetrodon* Linnaeus and *Chilichthys* Müller).

Cirrisomus Sprengleri Bonaparte 1841:second page of discussion of *Lagocephalus,* (after Swainson and Bloch, *Sprengleri* misspelling of *spengleri* Bloch).

Cirrisomus spengleri. Goode 1879:109 (reported, but not seen, from St. John's River).

Tetraodon marmoratus (not of Lowe or Valenciennes). Ranzani 1840:72 (original description, Brazil).

Anchisomus spengleri. (Kaup) Richardson 1854:162 (included in Kaup's manuscript list of species of *Anchisomus*).

Sténométope spengleri (Bibron) Duméril 1855:278 (included in Bibron's manuscript list of species of Sténométope, after Bloch).

Stenometopus spengleri. (Bibron) Troschel 1856:88 (after Duméril).

Crayracion spengleri. Bleeker 1865:65 (establishes *spengleri* as type of *Crayracion,* as *Crayracion laevissimus* Klein (=*T. spengleri* Bloch), see discussion below). Kner 1867:410 (Rio de Janeiro, Brazil).

Crayracion laevissimus (Klein) Bleeker 1866:18 (given as type of *Crayracion*).

Sphoeroides (also *Spheroides, Sphaeroides*) *spengleri.* Jordan and Edwards 1886:237 (synonymy, description, Texas, Florida, Brazil). Jordan 1886a:54 (Cuba) and 1886b:605 (in list of West Indian fishes). Jordan and Everman, 1898:1732 (synonymy, description, figure, West Indies, Texas, Florida, Brazil). Evermann and Marsh 1899:267 (Porto Rico). Schreiner and Ribeiro 1903:84 (Pernambuco, Brazil). Smith

1907:348 (synonymy, key, description, ecology, Massachusetts, North Carolina). Sumner, Osburn, and Cole 1911:762 (vicinity of Woods Hole, Massachusetts). Nichols 1914:82 (description, Katama Bay, Massachusetts to Key West, Florida). Ribeiro 1915:fifth page of Tetrodontidae section (description, Greater Antilles to Rio de Janeiro), and 1918:66 (Brazil). Breder 1927:79 (Bahamas). Meek and Hildebrand 1928:815 (key, description, Panama). Jordan, Evermann, and Clark 1930:498 (check list, Atlantic). ? Fowler 1931b:50 (Port Aransas, Texas, reference likely refers to *S. parvus*). Beebe and Tee-Van 1933:245 (description, Bermuda). Longley and Hildebrand 1941:300 (Tortugas, Florida). Fraser-Brunner 1943:11 (as a principal species of the genus). Fowler 1944:numerous citations (various Caribbean collections). Breder 1948:232 (key, figure, description). Puyo 1949:252 (description, French Guiana). Schultz 1949:95 (key). Baughman 1950:256 (Texas). Fowler 1953:72 (Colombian Caribbean). Hildebrand 1954:34 (ecology, Yucatan, Campeche snapper banks). Reid 1954:71 (ecology, Cedar Key, Florida). Hildebrand 1955:218 (ecology, Campeche). Briggs 1958:300 (Massachusetts to Brazil, after authors). Le Danois 1959:200 (systematics, in part). Bailey et al. 1960:49 (check list, Atlantic). Springer and Woodburn 1960:89 (ecology, Tampa, Florida). Durand 1961:59 (ecology, Guianas). Tabb and Manning 1961:642 (ecology, Florida). Bullis and Thompson 1965:61 (catch records). Cervigon 1965:68 (Venezuela), and 1966:839 (key, description, Venezuela). Randall 1967: 818 (feeding habits). Böhlke and Chaplin 1968:689 (key, figure, description, ecology, Bahamas). Randall 1968:278 (description, ecology, Caribbean). Shipp and Yerger 1969:484 (key, figure, Atlantic Ocean). Bailey et al. 1970:64 (check list, Atlantic).

Orbidus spengleri. Bean 1888:194 (Cozumel, Yucatan).

Discussion of Synonymy: *Sphoeroides spengleri* is a wide-ranging form which was collected frequently by voyages to the Americas as early as the eighteenth century. The species was described prior to Linnaeus' "Systema Naturae", by Klein (1744:18 and tab. III. f. 5). Seba (1758:III, 57-60, plate XXIII, 7 and 9) published excellent figures and description of the species synchronously with the appearance of "Systema Naturae", but assigned no binomial. Bloch (1785:135, pl. 144) published a diagnostic figure and description of the species, placed it in the genus *Tetrodon* of Linnaeus, and named the species *spengleri* after a Mr. Spengler of Copenhagen who presented Bloch with the type-specimen. The holotype has been examined and is presently deposited in the Institute für Spezielle Zoologie und Zoologisches Museum, Berlin.

Despite a profusion of various generic-specific combinations associated with this species, there has been remarkable stability in nomenclature and ease of identification of this form, due in part to the distinctive row of spots which borders the ventral margin of pigmentation. Only the similar

eastern Atlantic geminate, *Sphoeroides marmoratus,* has been consistently confused with *S. spengleri.* This form displays a similar border of spots.

Perhaps the most notable of misidentifications is attributable to Lacépède (1798, I:476-504, II:1-24). In this author's "Histoire Naturelle des Poissons", this single species was described under three names placed in two genera. The first reference was to Le Tetrodon spengleri, after Bloch. Then, from Plumier's manuscript, Lacépède published descriptions of Le Tetrodon Plumier and Le Sphéroide tuberculé. All three forms are conspecific; the latter two descriptions were based on different views of the same fish, as verified by Bloch's critical review of the Plumier manuscript (Bloch and Schneider 1801:509, 510, and Index, p. LVII). Although the specific names of Lacépède were little used in subsequent years, his error contributed a century of confusion in regard to establishment of a correct generic name (see discussion of synonymy under genus *Sphoeroides*).

Sphoeroides spengleri was not again described as new until Ranzani (1840:72) considered his Brazilian material to represent two undescribed species: *Tetraodon marmoratus* and *T. pachychephalus.* In referring to the work of Cuvier, Ranzani erroneously considered that both of his nominal species should be assigned to the second section of Cuvier's genus *Tetrodon,* that is, species with long heads. Since Cuvier included *T. spengleri* Bloch with the short-headed tetraodontids, Ranzani incorrectly considered his *T. marmoratus* as distinct from *T. spengleri* Bloch.

During the mid-19th century attempts to delineate generic relationships within the family resulted in the inclusion of *spengleri* with various generic groupings. Among these were *Cirrhisomus* Swainson, *Anchisomus* (Kaup) Richardson, *Stenometopus* (Bibron, Duméril) Troschel, and *Crayracion* (Klein) Bleeker. This latter grouping has led to complications regarding the availability of *Crayracion* as the proper generic name for the genus (see discussion of *Sphoeroides* synonymy). Bleeker (1865:65) properly considered the Crayracion laevissimus ex terreo rufescens of Klein as a synonym of *T. spengleri* Bloch. Later (1866:18), he established it as the type-species of *Crayracion,* a name from Walbaum (1792:580) but now considered unavailable.

Jordan and Edwards (1886:232) concluded that *Sphoeroides* (spelled *Sphaeroides*) was the correct generic name for the group, and subsequent references to the species have tended to follow Jordan and Edwards.

Material Examined: Fifty-nine series, 105 specimens.

Holotype: Deposited in Institute für Spezielle Zoologie und Zoologisches Museum, Berlin. Identified only, not measured. **North America:** ANSP 23879-91 (3, 39-43), Martha Vineyard, Mass. NMFS-G 41 (1, 133), FSU 1337 (2, 59-69), 4286 (5, 19-40), 4302 (1, 113), 8135 (1, 108), 10004 (1, 38), 10012 (1, 13), 10913 (1, 12), 10979 (2, 30-31), 11438 (3, 40-43), 11644 (1, 34), 11838 (1, 21), 11858 (7, 21-41), 11927 (2, 18-24), 14596 (17, 65-94), LACM 1472 (1, 22), UA 559 (1, 73), 561 (1, 63),

and UF 11733 (1, 127), 11793 (1, 25), Florida. ANSP 94632 (2, 115-122), Gulf between Florida and Cuba. NMFS-G BT 31 W 3 (1, 75), Gus 2 W 22 (1, 88), off Texas. **Central and South America:** GCRL 3021 (1, 74), off Mexico. GCRL 2965 (1, 101), Gulf of Campeche, Mexico. ANSP 78653 (1, 41), Honduras. TABL 67-97 (1, 63), off British Honduras. FSU 16684 (1, 68), Nicaragua. USNM 149705 (1, 53), GCRL 3283 (1, 72), 3695 (1, 19), Panama. ANSP 104555 (2, 111-112), 104557 (1, 119), 106748 (1, 67), off Colombia. RMNH 23511 (1, 60), EIMM (FCNC) 978 (1, 40), Venezuela. USNM 104323 (1, 92), Recife, Brazil. MZUSP 7695 (1, 34), Sao Paulo, Brazil. **Caribbean Islands:** ANSP (1, 98), UF 8997 (1, 72), 13965 (1, 11), 14044 (1, 67), Bahamas. UF 12137 (3, 22), Cuba. UF 15523 (1, 79), Grand Cayman Island. UF 15521 (1, 51), Jamaica. USNM 178031 (2, 80-94), Haiti. FSU 7729 (1, 59, 8980 (1, 51), 9084 (2, 61-65), UPR 2688 (2, 46-47), Puerto Rico. GCRL 1850 (1, 44), St. Thomas, Virgin Islands. ANSP 105426 (2, 62-74), St. Barthelemy, Lesser Antilles. RMNH 9853 (6, 26-41), St. Eustatius, Lesser Antilles, UF 12532 (1, 17), Willoughby Bay, Antigua, Lesser Antilles. ANSP 105387 (1, 27), Martinique, Lesser Antilles. ANSP 105352 (1, 102), Grenada, Lesser Antilles.

Diagnosis: *Sphoeroides spengleri* is a distinctively pigmented puffer, recognized by a discrete row of uniform round spots which bounds the ventrolateral body angle from chin to caudal peduncle. In addition, small flesh-colored lappets are present along the flanks and dorsum posterior to the pectoral fin. A black pair of lappets on the dorsum and distinct spots beneath the eye are both lacking; the absence of these distinguishes this form from its eastern Atlantic geminate, *S. marmoratus.* The caudal fin is strikingly marked by a black or very dark bar at its base and another at its posterior margin (Fig. 2). This pattern resulted in the designation of "Bandtail puffer" as its common name (Bailey et al. 1970:63).

General Description (Tables 2-4, 7): Head of adults 2.7 to 3 in SL, longer in subadults. Snout 1.6 to 2.1 in head, longest in adults, eye small, about 5 in head. Least bony interorbit slightly concave, moderate width, 3 to 4 in snout, about 6.6 in head. Dorsal and anal fins of near equal length, about 1.3 in snout, about 2.5 in head, and with their origins nearly opposite. Caudal truncate or very slightly rounded, short, with exposed length of medial rays about equal to snout length. Pectoral fins short, longest ray about 1.6 to 1.8 in snout length, about 3.2 in head. Dorsal rays 8, anal rays 7, pectoral rays 13 or 14 (not including a rudimentary base present at the upper fin sheath which may occasionally develop a rudimentary ray up to 25% the length of the first dorsal ray). Caudal rays 11, with the first upper and two lower rays unbranched.

Pigmentation is restricted to the dorsolateral surfaces. Basal pigmentation is uniform gray or brown, with a blotched, spotted or mottled appearance on the dorsum. The interorbit is marked by a dark bar of variable intensity, often with anterior and posterior extensions which

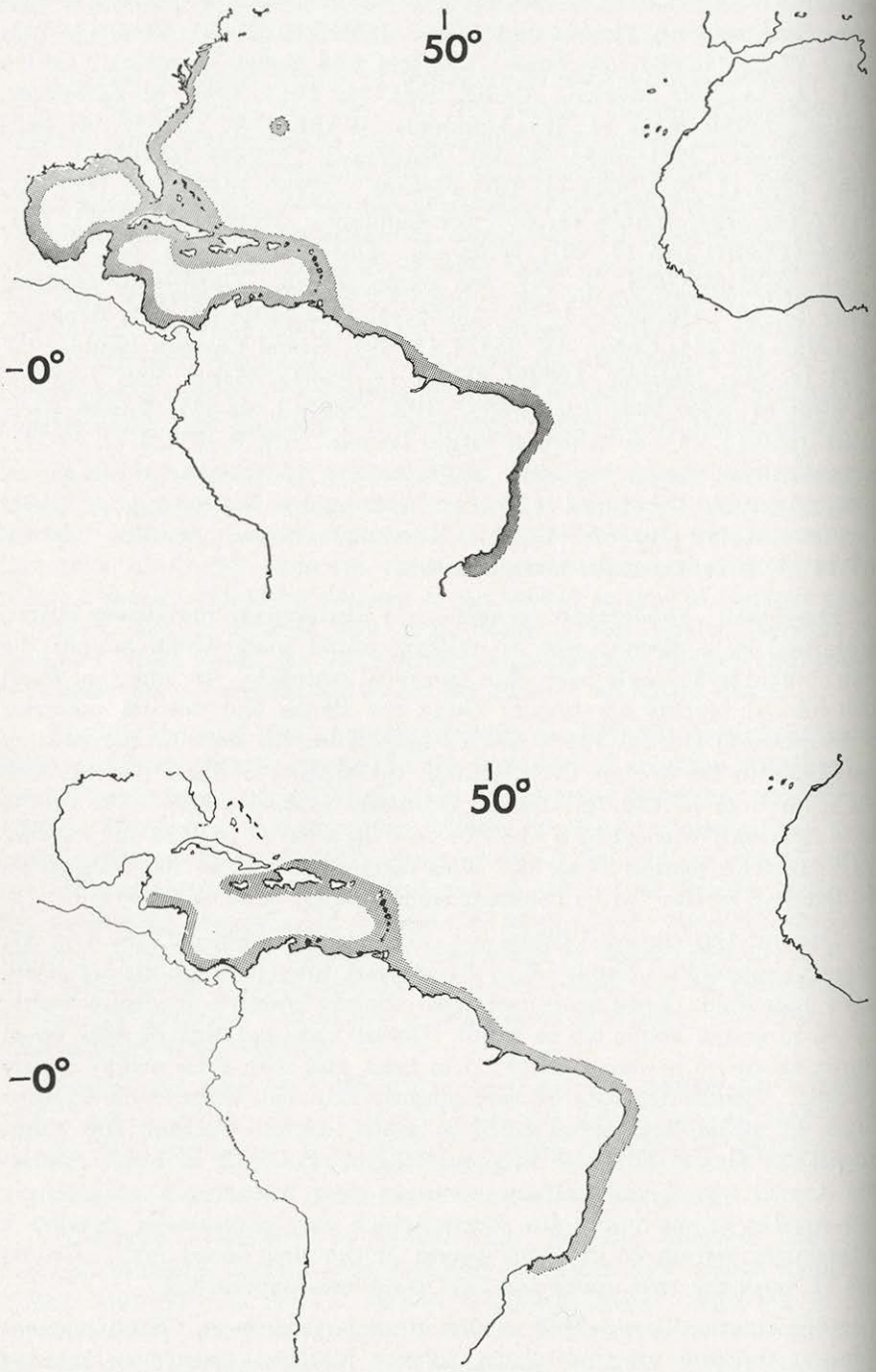

Figure 19. Upper: Distribution of *Sphoeroides spengleri*. Lower: Distribution of *S. greeleyi*.

result in a cross-shaped marking. The lateral surface is bounded ventrally by a distinct row of 11-14 sharply defined round spots, which extends from chin to caudal peduncle, occasionally with some loss of intensity in the more posterior spots. Immediately above this row is a region of light pigmentation which also extends from chin to peduncle, and in some well marked individuals may give the appearance of a light streak. Above this area is the typically mottled dorsal pigmentation. Occasionally two distinct dark spots are present in this mottled area anterolateral to the dorsal fin. The caudal displays a distinctive barred pattern, with a dark bar on the basal third of the fin, followed by a light bar, then finally another dark bar, all of nearly equal widths (Fig. 2). Other fins are nearly devoid of pigmentation.

Lappets are present along the lateral and dorsolateral surfaces posterior to the pectoral fins. These small (1-4 mm), fleshy, tan flaps are most concentrated about the level of the dorsal fin, and are evident in specimens as small as 20 mm SL.

Prickles are always present (but occasionally unexposed) on the ventral surface anterior to the anus. Dorsally they may be absent, but if present, are restricted to a small area between the nape and dorsal fin origin. Prickles are rarely present laterally, but may occur as a narrow strip on the lower cheek.

Largest specimen examined had a total length of 160 mm (about 6½ inches). Literature records which indicate a greater length for this species (Jordan and Evermann, 1898:1732; Smith, 1907:348) have apparently confused this species with other forms.

Geographic Variation: Specimens from insular populations may exhibit some variation in pigmentation of the spots which bound the ventrolateral body angle; the ventralmost margins of these spots may be slightly diffuse, and extend onto the belly itself. In mainland populations these spots are usually well defined and terminate abruptly at the ventrolateral body angle. In addition, insular populations usually display greater contrast between light and dark pigmentation. Ecological data of collections are insufficient to determine whether this difference is due to variance in bottom types, or if it is truly characteristic of the different regions.

Ecology and Distribution: *Sphoeroides spengleri* is a well known species, most often taken from clear, shallow, tropical water. Böhlke and Chaplin (1968:689) noted this species as the most common of the genus in their Bahaman collections. Further, they noted the usual presence of turtle grass at collection sites. Their suggestion that this is a preferred habitat is verified by collections examined by me from areas other than the Bahamas. Tabb and Manning (1961:642) have taken this species in salinities of 16 o/oo, and temperatures of 17-30° C. Stomach contents are similar to other congeneric species: principally crabs, small mollusks, and echinoderms. Randall's findings (1967:818) confirm stomach content analysis.

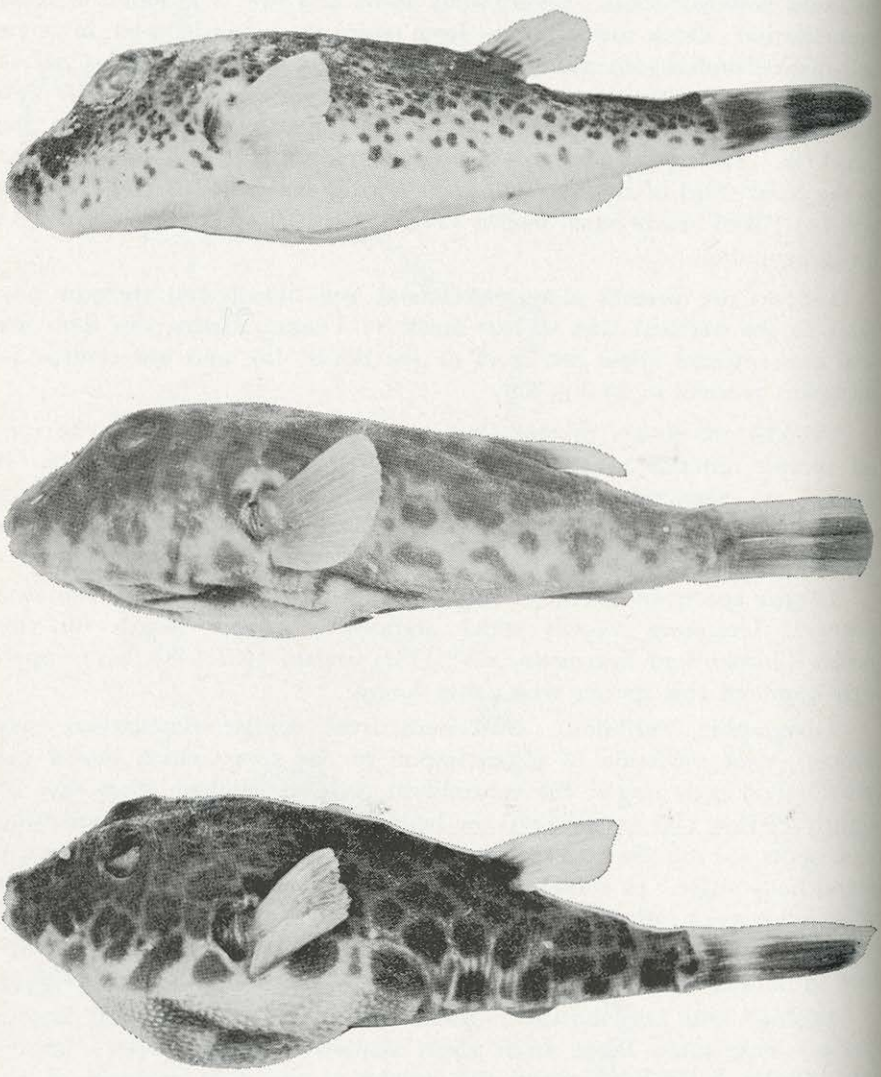

Figure 20. Variation in pigmentation in *Sphoeroides greeleyi.* Upper: ANSP 105345 (94 mm SL), Martinique, Lesser Antilles. Middle: ANSP 105681 (98 mm SL), Venezuela. Lower: MZUSP 3673 (59 mm SL), Rio de Janeiro, Brazil.

Although a shallow water form, in many localities *S. spengleri* appears to be replaced in extremely shallow, partially freshwater habitats by other species, especially *S. testudineus.* Catch records indicate that individuals may also sometimes inhabit deeper water. Durand (1961:59) listed specimens from the Guianas taken in 30 to 40 fathoms. *Sphoeroides spengleri* could be expected to be taken with any other western Atlantic member of the family except *Sphoeroides pachygaster* and *Lagocephalus lagocephalus.*

Records of *S. spengleri* north of extreme southern Florida are few. Although the species ranges from Massachusetts to Sao Paulo, Brazil, it is common only in the Caribbean Sea, peninsular Florida, the Bahamas, and Bermuda (Fig. 19).

Sphoeroides greeleyi Gilbert Caribbean Puffer
(Figs. 19 and 20)

Crayracion pantherinus (not of Eydoux and Souleyet) Kner 1867:407 (description, Rio de Janeiro).

Spheoroides (also *Sphaeroides*) *greeleyi* Gilbert 1900:176 (original description, figure, near Maceio, Brazil). Fowler 1941:182 (Brazil). Böhlke 1953:145 (lists holotype and paratype with collection data in the Natural History Museum of Stanford University). ? E. Le Danois 1961:123 (British Guiana). Randall 1968:279 (ecology, taxonomy, Caribbean).

Sphoeroides (also *Spheroides, Sphaeroides*) *adspersus* Schreiner and A. Ribeiro 1903:71, 84 (original description, Pernambuco, Brazil). A. Ribeiro 1915:page 8 of Tetrodontidae section (description, Brazil) and 1918:67 (synonymy, Brazil). Fowler 1941:183 (Brazil). Ribeiro 1961:6 (Brazil).

Tetrodon (*Sphoeroides*) *eulepidotus* Metzelaar 1919:170 (original description, figure, Lesser Antilles).

Sphoeroides eulepidotus. Jordan, Evermann, and Clark 1930:498 (check list, Caribbean). Schultz 1949:196 (key, description, taxonomy, Texas (?, see discussion of synonymy), Panama, West Indies, Rio de Janeiro). Wiebezahn 1955:248 (Venezuela). Cervigon 1965:68 (Venezuela) and 1966:841 (key, description, el Rincon, Venezuela).

S. marmoratus (not of Ranzani) Meek and Hildebrand 1928:813 (key, description, Fox Bay, Colon, Panama). ? Puyo 1949:250 (description, French Guiana, not of Ranzani).

Stenometopus latero-laevis (Bibron) Y. Le Danois 1959:195 and 1961:471 (as junior synonym of *S. testudineus*).

Discussion of Synonymy: *Sphoeroides greeleyi* was first described in the literature (Kner 1867:407) as *Crayracion pantherinus,* a species of

Indo-Pacific puffer described by Eydoux and Souleyet (1841:215). This latter species is an Indo-Pacific form, possibly a species of *Torquigener* (sensu Fraser-Brunner) and bears only a superficial resemblance in pigmentation to *Sphoeroides greeleyi.* But the adequate description of Kner leaves no doubt that the species he had in hand was *S. greeleyi.*

Gilbert described and figured *Sphoeroides greeleyi* as new in 1900 (p. 176), based on two specimens (112 and 105 mm total length) taken from a coral reef near Maceio, Brazil, by the Brunner-Agassiz expedition. I have examined the smaller (paratype) specimen, which is well preserved. Randall (1968:279) suggested that *S. greeleyi* is conspecific with the form common to the southern Caribbean, hitherto most commonly known as *S. eulepidotus* (Metzelaar). Although great pigmentation variation is exhibited between populations from the southeastern (Brazil) and northwestern (Venezuela, Central America) limits of the species range, I concur with Randall.

Sphoeroides adspersus was described by Schreiner and Ribeiro in 1903 (p. 71), based on three specimens from Pernambuco, Brazil. Although I have not examined any of the three cotypes which are deposited in the Museu Nacional in Brazil (Ribeiro 1961:6), I have examined a number of specimens whose identity was determined as *S. adspersus* by Ribeiro, junior author of the species' original description, and find them to be *S. greeleyi.* Based on this evidence I consider *S. adspersus* to be a junior synonym of *S. greeleyi.* Subsequent citations which included the name *S. adspersus* were based largely on material collected by Schreiner and Ribeiro.

The name most commonly assigned to *Sphoeroides greeleyi* in recent years has been *S. eulepidotus* of Metzelaar (1919:170). Metzelaar's excellent figure and adequate description leave no doubt as to the form he possessed. Apparently Gilbert's earlier description was overlooked, or perhaps the considerable variation between pigment patterns of Metzelaar's figure of *S. eulepidotus* and that of *S. greeleyi* by Gilbert convinced authors of the distinctness of the two forms. However, I can find no reference to *S. greeleyi* in the literature after the original description other than Fowler's Brazilian species list (1941:182), Böhlke's list of Stanford types (1953:143), a photograph of *S. nephelus* incorrectly labelled *S. greeleyi* in E. Le Danois' "Fishes of the World" (1961:123), and the erroneous synonymy of the name under *Sphaeroides punctatus* (Bloch) by LeDanois (1959:197).

Schultz (1949:196) recorded *S. eulepidotus* from Texas based on specimens present in the National Museum of Natural History collection. I have examined several USNM series of puffers from Texas labeled *S. eulepidotus,* and find them to be specimens of *S. parvus.*

Meek and Hildebrand (1928:813) used the name *S. marmoratus* in connection with this species. They noted the "distinctness of the scale-

like dermal development" on sides of head and body on their *S. marmoratus.* Metzelaar (1919:170) emphasized a similar comment in his original description of *S. eulepidotus.* Although neither Meek and Hildebrand's figure nor description is completely diagnostic, I have examined two of their specimens (FNHM 19538-19539) identified as *S. marmoratus* and find them conspecific with *S. greeleyi.*

Puyo (1949:250) described a species of *Sphoeroides* (as *S. marmoratus*) which is difficult to place. Although the diagnosis is inadequate for positive identification, pigmentation characters and pectoral ray counts indicate that it may be *S. greeleyi,* and it is thus included as a questionable synonym.

Le Danois (1959:159) included *Stenometopus latero-laevis,* an unpublished manuscript name of Bibron, in junior synonymy under *Sphaeroides testudineus.* I have examined Bibron's type material, and find it to be *S. greeleyi.*

Material Examined: Forty-five series, 122 specimens.

Types: CAS-SU 6308 (1, 80), coral reef, near Maceio, Brazil, paratype of *S. greeleyi.* MNHN B 1496 (1, 74), Brazil holotype of *Stenometopus latero-laevis* (Bibron) Le Danois. **Central America:** TABL 67-162 (1, 79), 67-166 (2, 70), off British Honduras. TU 24854 (1, 20), Costa Rica. FNHM 19538-19539 (2, 50-61), GCRL 10486 (3, 21-45), Panama. **South America:** BMNH (3, 73-99), Cartagena, Colombia. BMNH (1, 137), Puerto Cabella, Venezuela. ANSP 104606 (2, 134-139), 105179 (1, 114), 105681 (1, 98) Golfo de Cariaco, Venezuela. EIMM F. C. 1380 (1, 107), 1381 (1, 60), 1900 (1, 138), EIMM R.O.S. 973 (1, 134), Venezuela. BMNH (2, 115-139), Telron Bay, Trinidad. ANSP 93864 (2, 29-32), Trinidad. GCRL 9530 (1, 16), 9531 (1, 68), 9533 (2, 45-75), 9535 (34, 42-70), 9539 (2, 10-17), Bahia, Brazil. ANSP 1108 (1, 63), BMNH (1, 91), RMNH 16345 (1, 77), and USNM 23255 (1, 80), Rio de Janeiro, Brazil. MZUSP 2366 (1, 43), 3671 (2, 24-79), 3673 (3, 44-79), Est. de Rio, Brazil. MZUSP 2363 (2, 85-105), Sao Paulo, Brazil. MZUSP 776 (7, 48-97), Santos, Brazil. BMNH (1, 80), Brazil. **West Indian Islands:** LACM 5961 (4, 57-81), 5962 (2, 89-91), 6136 (14, 13-43), and BMNH (1, 124), Jamaica. ANSP 101834 (4, 32-62), 23598-604 (4, 55-80), UPR 1393 (1, 65), and USNM 126191 (1, 85), Puerto Rico. ANSP 105345 (2, 69-94), Martinique, Lesser Antilles. BMNH (1, 80), Tobago. **Canary Islands:** ? MNHN B 1512 (1, 81), Canary Islands.

Diagnosis: *Sphoeroides greeleyi* is recognized by its dorsal and lateral pigmentation pattern of spots and blotches of various sizes and shapes but near uniform intensity against a light basal color. A few lappets are present along the lateral surface, except in a few specimens from extreme northern (British Honduras) and southern (southeastern Brazil) limits of its range, which lack lappets. Posterior to the pectoral fin base is an area where distinctive dermal scale-like structures are developed. *Sphoe-*

roides testudineus, similar in pigmentation to *S. greeleyi,* always lacks lappets and the scale-like structures.

General Description (Tables 2-4, 8): Head of adults 2.7-2.9 in SL, slightly longer in subadults. Snout 1.7-2.2 in head; eye extremely variable, 4 to 8 in head, but usually about 5. Least bony interorbit flat to strongly concave, width variable, 2.5 to 4.8 in snout, about 6 to 9 in head; variance independent of size. Dorsal about 1.1 or 1.2 in snout, about 2.4 in head; anal a little shorter, about 1.3 in snout and 2.6 in head. Dorsal origin directly opposite anus, slightly rounded, moderately long with exposed length of medial rays about 0.8 in snout length, about 1.6 in head. Pectoral fins moderate, longest ray 1.2 to 1.4 in snout length, about 2.6 in head. Dorsal rays 8, anal rays 7, pectoral rays 14 or 15 (rarely 13 or 16). Caudal rays 11, with the first (and rarely second) upper and two lower rays unbranched.

Pigmentation is restricted to the dorsolateral surfaces. Basal pigmentation is light cream, yellow, or gray covered with chocolate blotches of various sizes and shapes. The basal pigmentation is lighter on the flanks than on the dorsum, where it usually forms an indiscrete T-shape posterior to the nape (Fig. 10). The darker blotches are all of near equal intensity, and may be irregularly but discretely defined, or may appear broken and fragmented. A slightly darker bar extends between the orbits. Caudal pigmentation varies from a barred pattern, similar to but not as distinctive as that of *Sphoeroides spengleri,* to a pattern of nearly uniform brown or yellow. Other fins may display slight pigmentation near their bases.

Fleshy, tan or light lappets are usually present, and most numerous on the posterolateral body surfaces, especially near the ventrolateral body angle.

Prickles are always present on the dorsal and ventral surfaces. Dorsally, prickles extend from between the nasal papillae or the interorbit posteriorly to the dorsal fin origin. On the ventral surface, prickles are present from the chin to or slightly beyond the anus, sometimes as far posterior as the anal fin origin. Laterally, prickles are usually absent, but occasionally the lower chin and lower flank just posterior to the pectoral fin may exhibit prickles.

Several authors have mentioned the presence of scale-like dermal development on this species. While dermal, imbricate scale-like structures can be seen on many *Sphoerides* (see discussion of phylogeny) they are especially evident in *S. greeleyi* and *S. parvus.* In both these forms, the lateral surfaces just posterior to the pectoral fins best display this development.

Sphoeroides greeleyi is a puffer of moderate size; the largest specimen examined measured 171 mm (about 7 inches) total length.

Geographic Variation: *Sphoeroides greeleyi* appears to exhibit greater

geographic variation than any other species of Atlantic tetraodontid. Individuals or populations from extreme northern (British Honduras), and southern (southeastern Brazil) limits of the range may occasionally lack lappets, or have but one or two lappets posterior to the pectoral fin along the ventrolateral body angle. Populations from more equatorial regions of its range, especially from mainland northern South America (Colombia, Venezuela) are extensively covered with lappets on the posterolateral surfaces. No other species of *Sphoeroides* includes populations with and without lappets.

Variation in pigmentation is extensive, but not totally a function of geography (Fig. 20). Populations from the east coast of central and south central Brazil include individuals with spots of relatively small size, about half the eye diameter, as well as individuals with very large spots, about twice the eye diameter. Most specimens from this region have most of the pigmented surface covered by the dark spotting. Populations from northern South American coasts usually display large, irregular shaped spots, slightly greater than eye diameter, but the most of the pigmented surface is of light background color. Populations from northern mainland areas (British Honduras) show further reduction in the dark pigmented spots, and more diffuse pigmentation. Insular populations display various patterns similar to mainland populations, with greater affinity with those from the east coast of Brazil. Individuals from insular populations also may display a unique variation of the spotted pattern in which the dark spots appear to be fragmented, resulting in many small associated clusters of dark spots. The surface area covered by the dark spotting may be partially correlated with size; juveniles have larger areas covered by the dark spots.

On the basis of material examined, the largest individuals are from Venezuela and Colombia.

Interorbit widths vary markedly between and within geographic populations. Individuals from Central America and northern South America have broader, less concave interorbital regions than insular and eastern Brazilian populations. However, there is extensive overlap between the zones.

Ecology and Distribution: *Sphoeroides greeleyi* is rarely taken in water more than a few meters in depth. It apparently occupies a niche close to that of the morphologically similar *S. testudineus,* as many of the specimens examined were removed from large series of the latter species. Based on numbers of individuals in these series, *S. testudineus* is more successful and is often taken in peripheral areas apparently inhospitable to *S. greeleyi* (see discussion of Phylogeny. Randall, 1968:279) noted a preference of *S. greeleyi* for mud and sand bottom.

The diet of the Caribbean puffer consists of sessile and slow-moving hard-shelled invertebrates. Sexual maturity is usually attained by specimens 80 mm SL.

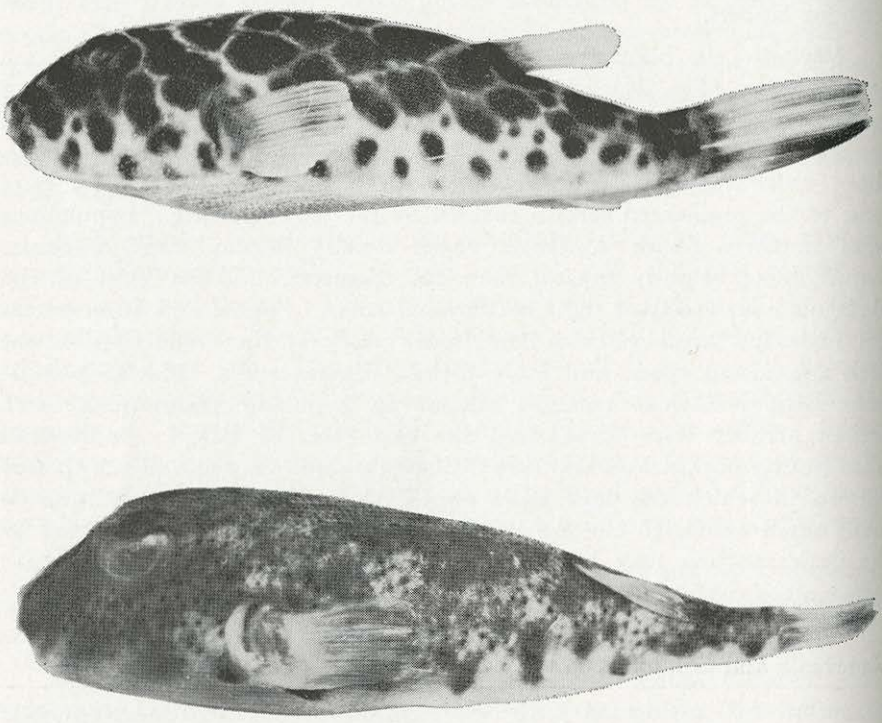

Figure 21. Upper: *Sphoeroides testudineus* FSU 11928 (96 mm SL), Jupiter Inlet, Florida. Lower: *S. maculatus* FSU 15478 (122 mm SL), North Carolina.

Sphoeroides greeleyi ranges from British Honduras throughout the Caribbean and South Atlantic to Santos, Brazil (Fig. 19). One specimen in the Museum National d'Histoire Naturelle in Paris is listed from "Canary Islands", but with no other data. Unless addtional material of this species is collected from the eastern Atlantic, this record must be considered doubtful.

Sphoeroides testudineus (Linnaeus) Checkered Puffer

(Figs. 14 and 21)

Tetraodon (also *Tetrondon*) *testudineus* Linnaeus 1758:332 (original description). Linnaeus 1766:410 (after Linnaeus 1758). Gmelin 1788: 1444 (after Linnaeus). ? Shaw 1804:444 (*T. testudineus* sensu Bloch is figured, but reference to Linnaeu is included). Günther 1870'282 (description, Caribbean, South America). Jordan and Gilbert 1883c: 861 (West Indies). Bean and Dresel 1885:151 (Jamaica). Lönneberg 1896:21 (holotype in the University of Uppsala). Beebe and Tee-Van 1928:266 (Haiti). Hildebrand and Schroeder 1928:349 (Chesapeake Bay, after Uhler and Lugger). Truitt, Bean, and Fowler 1929:102 (lower Chesapeake Bay. Nichols 1930:348 (Porto Rico). Nichols and Breder 1934:142 (accidental to Newport, Rhode Island, after Cope).

?*Tetrodon punctatus* Bloch and Schneider 1801:506 (original description, Brazil).

Tetrodon geometricus Bloch and Schneider 1801:508 (original description, Virginia, after Catesby).

Tetrodon batrachoides Freminville 1813:252 (original description, figure, Santo Domingo).

Chelichthyes punctatus. Müller and Troschel 1848b:641 (British Guiana).

Tetraodon ammocryptus Gosse 1851:287 (original description, ecology, Jamaica).

Holacanthus leionothos (Gronovius) Gray 1854:24 (description, American Oceans).

Tetraodon bajacu Castelnau 1855:98 (original description, figure, Bahia, Brazil).

Sténométope testudineus, Sténométope Pleii (Bibron) Duméril 1855:278 (included in Bibron's manuscript list of species of Sténométope, Sténométope testudineus after Linnaeus, Sténométope Pleii of Bibron).

Stenometopus testudineus, Stenometopus Pleii (Bibron) Troschel 1856: 88 (after Duméril).

Tetrodon punctatus Poey 1868:432 (original description, Cuba, also junior homonym of *T. punctatus* Bloch and Schneider).

Cirrisomus testudineus. Jordan and Gilbert 1878:366 (Atlantic Coast). Goode 1879:109 (St. John's River, Fla., listed but not actually seen).

Shoeroides (also *Spheroides, Sphaeroides*) *testudineus.* Jordan 1886a:54 Havana, Cuba, taxonomy). Jordan and Edwards 1886:239 (synonymy, description, West Indies north to Virginia, in part). Jordan 1886b: 605 (West Indies). Jordan and Rutter 1897:130 (Kingston, Jamiaca). Jordan and Evermann 1898:1734 (synonymy, description, figure, West Indies north to Rhode Island). Evermann and Marsh 1899:269 (key, description, ecology, Porto Rico). Evermann and Goldsborough 1902: 158 (description, Cozumel Island, Yucatan). Schreiner and Ribeiro 1903:84 (Pernambuco, Brazil). Fowler 1908:182 (New Jersey). Sumner, Osburn, and Cole 1911:763 (Newport, Rhode Island, after Cope). Starks 1913:63 (Natal, Brazil). Nichols 1914:82 (description, Miami, Guatemala, Brazil). Fowler 1915a:50 (Santo Domingo), and 1915b:541 (Trinidad, Grenada, St. Lucia). Ribeiro 1915:page 10, of Tetrodontidae section (key, description, Brazil). Fowler 1916b:405 (Canal Zone). Fowler 1917:136 (Panama). Jordan 1917: 15, 167 (review of generic types). Ribeiro 1918:67 (synonymy, Brazil). Wilson 1918:69 (Cartegena, Colombia). Breder 1925:142, 157 (ecology, Panama). Meek and Hildebrand 1928:817 (key, synonymy, description, figure, Panama). Fowler 1931a:405 (Trinidad). Hubbs 1936:248 (Campeche, Yucatan). Fowler 1941:83 (Brazil). Fraser-Brunner 1943:11 (listed as a principal species of *Sphaeroides*). Breder 1948:234 (key, description, figure). ? Baughman 1950:256 (Galveston, Texas). Fowler 1950:75 (figure, Old Providence). Fowler 1952:145 (Cape May, New Jersey), and 1953:72 (Colombia). Hildebrand 1954:320 (ecology, Campeche, Yucatan), and 1955:218 (Campeche, Yucatan). Wiebazahn 1955:248 (Venezuela). Briggs 1958:300 (Rhode Island to Sao Francisco do Sul, Brazil, Gulf of Mexico ?, after authors). Caldwell et al. 1959:28 (Costa Rica). Le Danois 1959:195 (systematics, in part). Bailey et al. 1960:49 check list, Atlantic). Y. Le Danois 1961:470 (list of types in Museum National d'Histoire Naturelle). Ribeiro 1961:6 (Brazil). Lowe (McConnell) 1962:697 (ecology, Surinam, British Guiana). Gunter and Hall 1963:226, 284 (ecology, Florida). Bullis and Thompson 1965: 61 (catch records). Cervigon 1965:68 (Venezuela). ? Parker 1965: 218 (Galveston Bay, Texas). Cervigon 1966:840 (key, description, Venezuela). Böhlke and Chaplin 1968:688 (ecology, key, description, figure, Bahamas). Gines and Cervigon 1968:38, 44, 74 (ecology, Guianas, Surinam). Randall 1968:278 (Caribbean). Shipp and Yerger 1969b:485 (key, figure). Bailey et al. 1970:64 (checklist, Atlantic). Nugent 1970:53 (Florida). Gilbert 1971:47 (ecology, Costa Rica).

Cheilichthyes testudineus. Uhler and Lugger 1877:59 (Chesapeake Bay). Jordan, Evermann, and Clark 1930:499 (check list, Caribbean, Atlan-

tic).

Orbidus testudineus. Jordan and Bollman 1888:553 (Bahamas).

? *Spheroides maculatus* (not of Bloch and Schneider) Puyo 1949:251 (French Guiana).

Discussion of Synonymy: *Sphoeroides testudineus* was the first species of *Tetraodon* assigned by Linnaeus in the tenth edition of "Systema Naturae" (1758:332). Because in many areas of tropical America it is the most common shallow water puffer and extremely easy to capture, this form has been extensively collected by exploring naturalists since the 18th century. The *Tetraodon testudineus* of Linnaeus is doubtlessly the same species to which the name is today applied. A diagnostic illustration is found in the "Amoenitates Acadamicae" of (Balk) Linnaeus (1749:309, Tab. 14, Fig. 3), a reference to which is included in the original species description. The holotype is in the collection of the University of Uppsala (Lönneberg 1896:21), but I have not examined it.

Bloch (1785:123, pl. 139) included a description of a *Tetrodon testudineus* (attributed to Linnaeus) with an accompanying plate. The *T. testudineus* of Bloch was not that of Linnaeus, but apparently a synonym of *Arothron reticulatus* (Bloch and Schneider 1801:506) from the Indo-Pacific (Tyler 1964:123). The "General Zoology or Systematic Natural History" of Shaw (1804) copied Bloch's description and figure, but includes reference to the *T. testudineus* of Linnaeus. The specific name *testudineus* has been correctly and most frequently applied to the western Atlantic species of Linnaeus since the time of Günther.

Tetrodon punctatus apparently has been applied to *S. testudineus* by Bloch and Schneider (1801:506) and indepedently by Poey (1868:432, see below). The brief description of the former contains incorrect fin ray counts (P. 18; A. 10; C. 10; D. 10) for the species, but such errors were frequent when mounted specimens were studied instead of those preserved in spirits. There is no other tetraodontid from the "Sea of Brazil" which would fit the "Nigro-punctato" of Bloch and Schneider's original description. *Colomesus psittacus,* has similar fin ray counts (P. 17-19; A. 10-11; C. 11; D. 10-11), but rarely reaches Brazil. It is a barred rather than spotted species, and is described by Bloch and Schneider as *T. psittacus* on the previous page (505) and figured as *T. psittacus* (Fig. 95). Three other spotted *Sphoeroides* (with fin ray counts similar to *S. testudineus*) appear in Brazilian Atlantic waters: *S. spengleri* (Bloch), *S. greeleyi* Gilbert and *S. tyleri* Shipp. *Sphoeroides spengleri* was treated on page 504 of Bloch and Schneider, and bears a distinctive row of intense spots not mentioned in the original description of *T. punctatus. Sphoeroides greeleyi* and *S. tyleri* are spotted with rich brown, rather than black. Therefore, it is reasonable to consider *T. punctatus* Bloch and Schneider at least as a questionable junior synonym of *T. testudineus* Linnaeus. It is possible that no specimen was available to Schneider when the description

was written, as it is not among Bloch's types in Berlin (Kurt Deckert, pers. comm.) however, no reference to previous authors follows the description.

Inclusion of *T. geometricus* (=*S. testudineus*) by Bloch and Schneider does not preclude its conspecificity with their previously treated *T. punctatus.* Because great variability exists between color patterns of different populations of this species, Bloch and Schneider may have concluded that their Brazilian *T. punctatus* was distinct from the North Atlantic Orbis laevis variegatus of Catesby.

Bibron's manuscript (partially published by Duméril 1855:274) refers to two specimens in the Museum National d'Histoire Naturelle, both identified by me as *S. testudineus.* The first, representing the type-species of the genus *Stenometopus,* is labeled Sténométope testudineus, the second, Sténométope Pleii. These names, Latinized by Troschel (1856:88) are junior synonyms of *S. testudineus.*

Sphoeroides maculatus Puyo (1949:25, not of Bloch and Schneider) is included as a doubtful synonym of *S. testudineus.* Puyo's specimens were taken from French Guiana, far from the range of *S. maculatus* of Bloch and Schneider (northeast Florida to Newfoundland). Puyo's description, while diagnostically incomplete, most nearly fits *S. testudineus,* a common species of French Guiana, and not otherwise mentioned in Puyo's work.

Material Examined: Ninety-nine series, 347 specimens.

Types: BMNH (1, 63), Jamaica, holotype of *Tetrodon ammocryptus* Gosse. MNHN A. 8344 (1, 131), Martinique, mounted, holotype of *Stenometopus Pleii* (Bibron) Troschel. MNHN 1513 (1, 71) ? "probably Mexico", holotype of *Tetrodon veracruzensis,* a manuscript name. MNHN B. 1485 (2, 57-177), unkown locality, "Genotypes" of Sténométope Bibron. **North America:** USNM 794 (1, 246), Beesley's Point, New Jersey. USNM 184266 (3, 79-164), GCRL 529 (1, 112), FSU 9097 (5, 122-135), 1027 (1, 77), 10884 (1, 82), 11928 (3, 87-96), and ANSP 78571 (2, 47-55), east coast of Florida. ANSP 97633 (2, 109-139), GCRL 2922 (2, 110-121), 2923 (5, 30-80), 2950 (7, 39-108), 2998 (20, 73-150), 3108 (1, 116), Campeche, Mexico. TABL 67-178 (1, 66), east Yucatan, Mexico. **Central America:** ANSP 97546 (1, 153), TABL 67-162 (11, 91-157), 67-165 (5, 102-148), 67-166 (5, 99-123), 67-167 (22, 77-136), British Honduras. GCRL 1352 (1, 20), Guatemala. GCRL 1358 (19, 35-66), Gulf of Honduras. GCRL 1470 (1, 116), Honduras. FSU 16683 (25, 56-97), Nicaragua. FSU 15963 (18, 82-109), TU 24854 (25, 20-59), Costa Rica. GCRL 1642 (4, 22-24), 1893 (1, 91), UMML P-449 (1, 143), 22526 (2, 51-59), Panama. **South America:** UMML P-351 (1, 114), 22881 (1, 95), off Colombia. USNM 3502 (2, 82-84), Gulf of Uraba, Colombia. USNM 121701 (2, 51-54), EIMM 973 (2, 101-135), EIMM 991 (1, 144), Venezuela. EIMM uncat. (1, 93), off British Guiana. RMNH 7352 (1, 124), RMNH uncat. (2, 116-158), Surinam. MZUSP 7673-7692 (20, 62-173), Sergipe, Brazil.

MZUSP 3241 (1, 70), Ilheus, Brazil. MZUSP 925 (8, 87-102), Bahia, Brazil. MZUSP 936 (19, 56-109), 3669 (6, 73-160), 3671 (8, 58-121), 3673 (1, 69), RMNH 16344-16345 (2, 146-192), Rio de Janeiro, Brazil. MZUSP 3196 (5, 72-99), 7696-7698 (3, 140-154), 7699-7706 (8, 91-147), Sao Paulo, Brazil. **Caribbean Islands:** ANSP 84658 (5, 132-153), Grand Bahama Island. UF 15522 (7, 63-161), Andros Island, Bahamas. RMNH 15470 (2, 145-164), Nassau Harbor, Bahamas. ANSP 84662 (15, 63-130), New Providence, Bahamas. ANSP 84660 (1, 158), Brigantine Cays Bahamas. USNM 94263 (1, 85), 192184 (3, 71-123), Havana, Cuba. ANSP 52054 (1, 109), UF 15520 (1, 125), Jamaica. RMNH 8462 (1, 125), Haiti. UPR 1398 (3, 51-133), Puerto Rico. GCRL 1849 (1, 68), St. Thomas, Virgin Is. GCRL 1917 (1, 87), St. John, Virgin Is.

Diagnosis: *Sproeroides testudineus* is a distinctively pigmented puffer, characterized by a dorsal pattern of discrete, coarse light arches and circular markings, one or two light interorbital bars (Fig. 10), and a heavily spotted lateral surface, spots usually about one-half eye diameter. Lappets are absent. *Sphoeroides greeleyi,* the only other species likely to be confused with *S. testudineus,* has lappets along the flanks.

General Description (Tables 2-4, 8): Head 2.7-3.0 in adults, slightly longer in subadults. Snout 1.9-2.3 in head, longest in adults. Eye 4 to 6 in head, usually about 4.5 to 5. Least bony interorbit flat or sometimes slightly concave, broad, 2 to 3.1 in snout, about 5.2 in head; interorbits of adults average a little broader than those of juveniles. Dorsal usually longer than snout, 0.8 to 1.1 in snout, about 2.2 in head; anal a little shorter, 1 to 1.2 in snout, about 2.3 in head. Dorsal fin origin directly opposite anus, slightly anterior to anal fin origin. Caudal slightly rounded, long, exposed length of medial rays about 0.7 in snout length, about 1.5 in head. Pectoral fins moderately long, longest ray about 1.1 to 1.2 in snout length, about 2.5 in head. Dorsal rays 8, anal rays 7, pectoral rays usually 14 or 15 (rarely 13, occasionally 16). Caudal rays 11, with the first upper ray and two lower rays unbranched.

Pigmentation is restricted to the dorsal and lateral surfaces. Basal pigmentation is usually brown, sometimes gray; dorsally it is of varying intensities, but fades or disappears laterally. Dorsally the basal pigmentation is traversed by a complex pattern of numerous, arching, coarse light streaks, or lines, some of which are always present and distinct, while others may be present in some individuals, absent in others, or vary in position and intensity. The most intense of these light markings are one or two bars which cross the interorbital region (Fig. 10). Frequently, distinct dark spots are found over the basal pigmentation. Numerous dark brown or black spots are always evident laterally, where the basal pigmentation is light or absent. These are of varying sizes, but most often about half eye diameter. In individuals from some populations, these spots appear conjoined, and produce a patterns of irregular, large lateral blotches. In very large individuals, the basal pigmentation of the

dorsum may be broken up into many spots of about equal diameter to the spots on the flanks. The distal half of the caudal fin is usually dark brown or black; the proximal half is light, except for a narrow diffuse basal bar. All other fins are uniformly straw-colored.

Lappets are never present. Prickles are always present on the dorsum, usually extending from the interorbit, or slightly anterior of the interorbit, to the dorsal fin origin, and ventrally from chin to anus. A broad band of prickles posterior to the pectoral fin usually connects dorsal and ventral prickled areas. Occasionally prickles may be located on the lower cheek. Although *S. testudineus* is relatively completely covered, the prickles are often unexposed and recognizable only by the minute openings through which they presumably protrude when extended. This condition is different than that of most other species.

Geographic Variation: Extensive variation in pigmentation in *S. testudineus* is not correlated to geography. Variation between populations several hundred miles apart may appear relatively great, but over great oceanic distances may be slight.

Some slight geographic variation was observed in other characters. Interorbital width averages slightly less in Central American populations (about 2.6 in snout length) than in North American, South American, and West Indian populations (about 2.4 in snout length); however, much overlap between regions is demonstrable. Individuals of Central American populations are small and mature at a smaller size than those of other areas. Females 80 mm SL extruding eggs were observed from Central America, while no mature females less than 110 mm SL were found in other areas. Males average smaller and mature at a slightly smaller size than females.

The largest specimen examined measured 246 mm total length (about 10 inches).

Ecology and Distribution: *Sphoeroides testudineus* is usually taken in shallow water, very frequently near mangroves. The deepest water from which I have specimens is 11 fathoms, but most specimens examined were from water less than 3 meters deep. Records of specimens from deeper water are doubtful. This species frequents bays and estuaries, and collections from "creeks" have produced *S. testudineus*, although no salinity data accompanied such collections. However, Gunter and Hall (1963:284) reported this species from nearly fresh water (0.36 o/oo) from the St. Lucie estuary of southeast Florida. These authors also reported capture of this species from a temperature range from 15.0° C. to 30.7° C. The presence of juveniles less than 20 mm SL in January, May, and November probably indicates a continuous reproduction period.

This species is extremely abundant from the Atlantic Coast of southern Florida, throughout the Caribbean Islands, Campeche Bay, and Central and South America to Santos, Brazil (Fig. 14). It has been taken as far

north as New Jersey, and possibly to Rhode Island. However, all references to its presence in Rhode Island are after Cope and I find no such reference of Cope's. However, he did list *Tetraodon geometricus* (=*S. annulatus*) and *T. trichocephalus* from Rhode Island (1870:120). These specimens were actually collected from the Pacific Ocean (probably Panama), and mistakingly mixed with Samuel Powell's collection of Rhode Island material. *Sphoeroides annulatus* is a closely related geminate of *S. testudineus,* sometimes considered conspecific (i.e. Le Danois 1959:195), while *S. trichocephalus* is a senior synonym of *S. jurthii* (Steindachner). Cope's erroneous record of *S. annulatus* has therefore probably led to its subsequent inclusion as *S. testudineus* in Rhode Island faunal lists (see such records in synonymy of *S. testudineus*). It is conspicuously absent from collections of the entire Gulf of Mexico except Campeche. Tabb and Manning (1961:642) failed to collect this species from Florida Bay. Records of specimens from elsewhere in the Gulf of Mexico could not be verified. Extensive collection by me from the southeastern (Ft. Myers, Florida) to the northwestern Gulf (Galveston, Texas) failed to reveal a single specimen of *S. testudineus,* despite samplings in appropriate habitats, and successful capture of many other *Sphoroides* (*S. nephelus* and *S. parvus*). Competitive exclusion by these two species may influence the range and abundance of *S. testudineus* in the northern hemisphere.

Sphoeroides maculatus (Bloch and Schneider) Northern Puffer

(Figs. 21 and 22)

Tetrodon hispidus (not of Linnaeus) Schöpf 1787:189 (description, Long Island, New York).

Tetrodon hispidus var. *maculatus* Bloch and Schneider 1801:504 (after Schöpf).

Tetraodon (also *Tetrodon*) *turgidus* Mitchill 1815:473 (original description, figure, New York). Cuvier 1829:369 (after Mitchill). Storer 1839:169 (Massachusetts). Ayres 1842:285 (New York). DeKay 1842:327 (description, figure, New York). Storer 1846:241 (North America). Baird 1855:352 (New Jersey). Günther 1870:285 (description, New York, in part). Bean 1880:76 (New England). Jordan and Gilbert 1883a:861 (North America). Bean 1887:133 (New Jersey). Jenkins 1887:93 (Beaufort, North Carolina). Nelson 1890: 768 (New Jersey). Wilson 1900:355 (Beaufort, North Carolina).

Sténométope binummulatus (Bibron) Duméril 1855:278 (included in Bibron's manuscript list of species of Sténométope).

Stenometopus binummulatus (Bibron) Troschel 1856:88 (after Duméril).

Gastrophysus turgidus. Abbott 1868:827 (New Jersey).

Chilichthys (also *Chilichthyes*) *turgidus.* Gill 1873:793 (Cape Cod to Florida). Uhler and Lugger 1876:73 (Maryland). Yarrow 1877:

204 (Beaufort, North Carolina).

Cirrisomus turgidus. Jordan and Gilbert 1878:366 (Beaufort, North Carolina).

Sphoeroides (also *Spheroides, Sphaeroides*) *maculatus.* Jordan and Edwards 1886:238 (synonymy, description, Cape Ann, Massachusetts to northern Florida). Jordan and Evermann 1898:1733 (synonymy, description, figure, Cape Ann to Florida). Fowler 1905:364 (New Jersey). Linton 1905:402 (parasitology, Beaufort, North Carolina). Smith 1907:347 (synonymy, key, description, figure, ecology, North Carolina). Sumner, Osburn, and Cole 1911:762 (Woods Hole, Massachusetts). Fowler 1911:3 (Maryland). Kendall 1914:56 (Maine). Nichols 1914:82 (description, Massachusetts to North Carolina), Murphy and Harper 1915:42 (Long Island, New York). Fowler 1916a:10 (New Jersey). Latham 1917:22 (Long Island, New York). Fowler 1919b:14 and 1920:164 (New Jersey). Townsend and Nichols 1921:11 (New York). Welsh and Breder 1922:261 (ecology, life history). Bigelow and Welsh 1924:298 (ecology, figure, description, Maine). Fowler 1925:42, 46; 1926:150, and 1927:614 (New Jersey). Parr 1927:245 (functional anatomy). Hildebrand and Schroeder 1928:248 (Chesapeake Bay). Jordan, Evermann, and Clark 1930:498 (check list, Cape Ann to Florida). Breder 1932:32 (Rhode Island). Fowler 1937:308 (New Jersey). Fraser-Brunner 1943:11 (listed as a "principal species" of *Sphaeroides*). Merriman 1947:286 (life history, Connecticut). Breder 1948:232 (key, description, figure). Fowler 1952:144 (New Jersey). Bigelow and Schroeder 1954:526 (ecology, figure, description, Maine). Briggs 1958:300 (Nova Scotia to Florida; northern Gulf of Mexico ?, after authors). Bailey et al. 1960:49 (check list, Atlantic). Bullis and Thompson 1965:61 (catch records). Breder and Rosen 1966:592 (life history). Liem and Scott 1966:415 (Newfoundland to Maine). Wilbur and Schneider 1967: 63 (ontogeny). Shipp and Yerger 1969a:425 (systematics, figures, Newfoundland to Marineland, Florida), and 1969b:484 (key, figure). Bailey et al. 1970:63 (check list, Atlantic). Richards and Castagna 1970:235 (ecology, Virginia). Dovel 1971:1 (spawning habits, Chesapeake Bay). Winterbottom 1971:1 (functional anatomy).

Orbidus maculatus. Moore 1892:363 (New Jersey).

Tetraodon (also *Tetrodon*) *maculatus.* Truitt, Bean, and Fowler 1929: 102 (Chesapeake Bay). Nichols and Breder 1934 (New England).

Tetrodon punctatus (not of Bloch and Schneider) Y. Le Danois 1959:196 systematics, in part) and 1961:471 (list of types in Museum National d'Histoire Naturelle).

Discussion of Synonymy: The first published description of *Sphoeroides maculatus* was by Schöpf (1787:189), based on material from Long Island, New York, Schöpf assigned the form to *Tetrodon hispidus* of

Linnaeus, because according to DeKay (1842:328) "(Schöpf) was afraid to make an assertion when it contradicted, or was not supported by the authority of Linnaeus . . ., and referred it (*S. maculatus*) to the *T. hispidus,* a very different species. It was this species that Schoepff asserts to be furnished with lungs lying in the fore part of the breast, having mistaken the kidneys for lungs."

Bloch and Schneider (1801:504) based their original description of this species after Schöpf, and referred to Schöpf's reference of a variation of *T. hispidus* with lungs "Pulmones in hoc pisce vidisse se refert Schoepf Schrift VIII." However, since Bloch and Schneider apparently had no specimen in hand (no type exists among Bloch's other types), they merely designated the species as a variety of *T. hispidus.* "Var. maculatus. T." Jordan and Edwards (1886:238) ultimately considered this (*maculatus*) to be the specific name, which is in accord with the International Code of Zoological Nomenclature, Article 17 (9).

Previous to Jordan and Edward's 1886 work, Mitchill's (1815:473) description of this species as *Tetrodon turgidus* had gained near universal acceptance by ichthyologists. In the interim, only Bibron's manuscript name (Sténométope binummulatus) published in French by Duméril 1855:278) and Latinized a year later by Troschel (1856:88), had applied to this form (based on a mounted specimen from "Philadelphia" in the Museum National d'Histoire Naturelle, Paris, which I have examined). However, since most of Bibron's names lacked accompanying description they have never seriously been considered as valid until Le Danois (1959) recently resurrected many of them. In any case *Tetrodon turgidus* Mitchill and *Stenometopus binummulatus* (Bibron) Troschel are junior synonyms of *S. maculatus.*

Various other genus-species combinations have been used for *Sphoeroides, maculatus.* Goode's (1879:109) record of *Cirrisomus turgidus* from Jacksonville, Florida is in doubt as no description accompanied the record. This locality is in a zone of sympatry of *S. maculatus* and *S. nephelus,* a species frequently confused with *S. maculatus* in the past. The alleged presence of *S. maculatus* in the Gulf of Meixco (Baughman 1950:256; Briggs 1958:300) is almost certainly based on misidentified specimens, probably of *S. parvus.*

LeDanois (1959:196) condensed a number of closely and distantly related western Atlantic species of *Sphoeroides* under the single designation *Sphaeroides punctatus* (Bloch and Schneider). *Tetrodon punctatus* Bloch and Schneider, probably referring to *S. testudineus* (see discussion of synonymy under *S. testudineus*), is described on p. 506 of Bloch and Schneider's Systema Ichthyologiae (1801), two pages after the description of *Tetrodon hispidus* var. *maculatus.* In addition, *T. punctatus* was noted by its authors as from the Sea of Brazil, while *S. maculatus* extends no further south than northeast Florida. In short, the *Tetrodon punctatus* of Bloch and Schneider is not the *Sphoeroides maculatus* (Bloch and

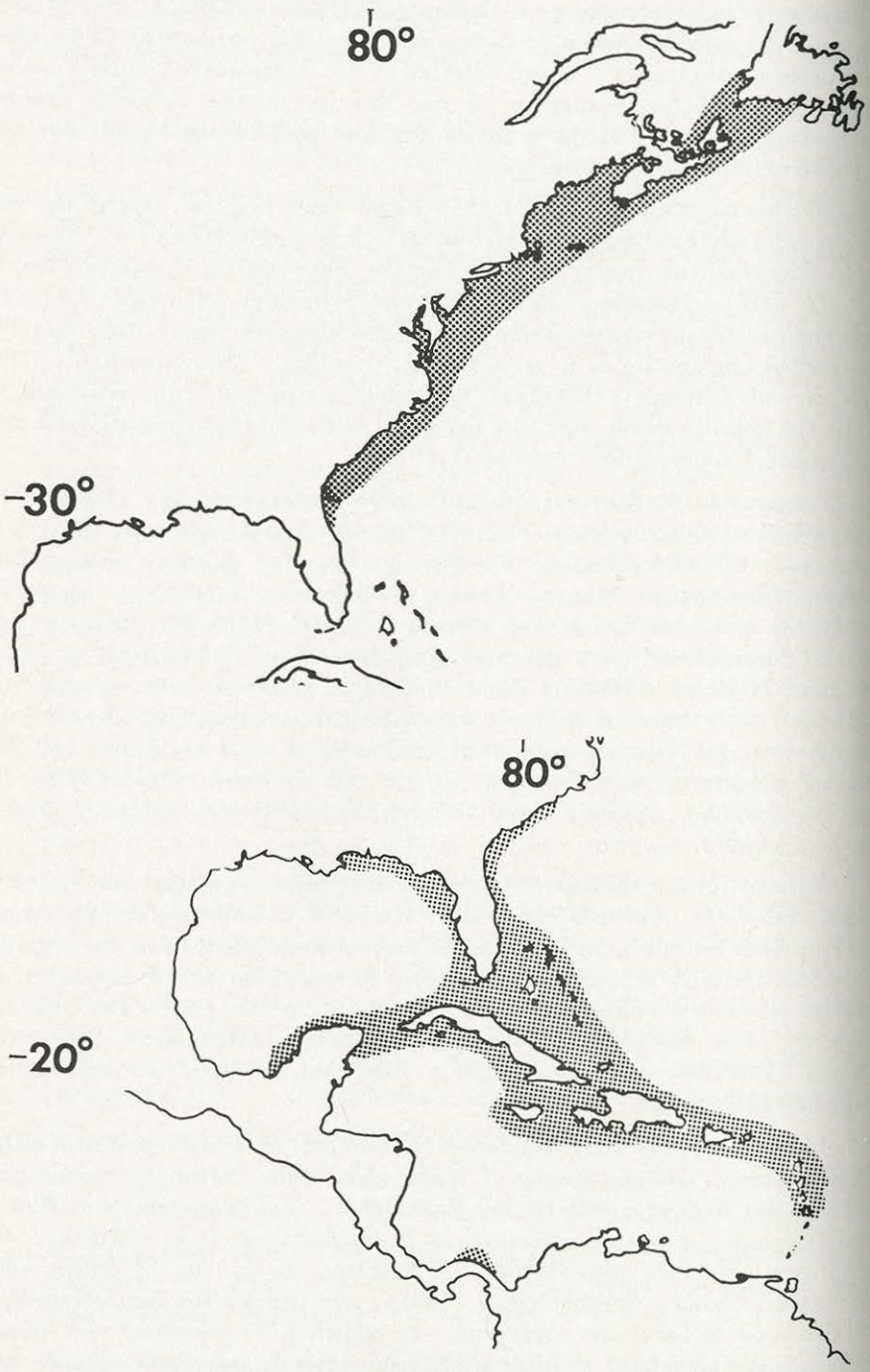

Figure 22. Upper: Distribution of *Sphoeroides maculatus*. Lower: Distribution of *S. nephelus*.

Schneider) of the Atlantic coast of North America.

Material Examined: Forty-five series, 220 specimens.

Types: UF 12303 (1, 146), neotype of *Sphoeroides maculatus* designated by Shipp and Yerger (1969a:426), from Long Island. MNHN 8359 (1, 179), "Philadelphia", mounted, holotype of *Stenometopus binummulatus* (Bibron) Troschel. **North America:** USNM 22771 (2, 74-147), TU 19744 (3, 155-165), Massachusetts. USNM 154810 (1, 153), Connecticut. UA 79 (4, 69-78), New York. USNM 26432 (1, 122), 223089 (1, 100), 223091 (1, 142), Maryland. USNM 3169 (1, 85), 43154 (1, 113), FSU 13876, 13877 (25, 83-192), Virgina. UA 86 (1, 129), 1446 (1, 114), FSU 5311 (1, 110), 13878 (23, 150-218), 15476 (1, 127), 15477 (2, 121-134), 15478 (3, 88-122), 16717 (4, 97-119), 16718 (15, 98-138), 16719 (5, 99-141), 16720 (4, 83-103), 17523 (skull), and UF 11787 (2, 135-145), Noth Carolina. UG uncat. (2, 130-185), FSU 13879 (2, 52), TABL uncat. (8, 15-26), (5, 13-25), (56, 12-24), (16, 12-24), Georgia. UF 11788 (2, 10), 11789 (7,13-45), 11791 (3, 14-32), 11792 (1, 20), FSU 10800 (1, 217), Northeast Florida. USNM 156488 (1, 164), 156489 (2, 87-110), UF 11772 (1, 150), 11773 (5, 129-172), 11774 (2, 180-182), offshore Atlantic, North Carolina to Georgia.

Diagnosis: *Sphoeroides maculatus* is easily recognized by the presence of vertical or slightly diagonal dark bars along the flanks, posterior to the pectoral fin. In addition, adults bear many tiny (about 1 mm) jet black "pepper" spots along the upper lateral and dorsal surfaces. Lappets are absent, but the body is densely covered with close set prickles which extend posteriorly beyond the anal opening.

General Description (Tables 2-4, 8): Head 2.7 to 3 in SL in adults, longer in subadults. Snout 1.7 to 2.1 in head, longest in adults. Eye 4 to 8 in head, but most often large, about 5 in head. Least bony interorbit flat to slightly concave, moderately broad, 2.5 to 4 in snout, usually about 3.3 in snout, about 6.5 in head; interorbits of adults average slightly broader than juveniles. Dorsal slightly shorter than snout, usually 1.1 to 1.2 in snout, 2.3 in head, anal a little shorter, 1.2 to 1.5 in snout, 2.6 in head. Dorsal fin origin opposite posterior edge of anal opening, slightly anterior to anal fin origin. Caudal truncate or slightly rounded but often with the uppermost rays longest. Length of exposed medial caudal rays about equal to snout length, about 2 in head. Pectoral fins moderately long, about 1.3 in snout, 2.5 in head. Dorsal rays 8, anal rays 7, pectoral rays usually 15 or 16 (rarely 17). Caudal rays 11, with the first upper and two lower rays usually unbranched.

Pigmentation is restricted to dorsolateral surfaces. Basal pigmentation is usually gray, which fades laterally. Poorly defined black spots cover the dorsal surfaces, and a vague dark bar traverses the interorbital region. A vague dark saddle extends transversely across the dorsum and passes through the base of the dorsal fin. Another similar saddle is pres-

ent across the dorsal area of the caudal peduncle. Tiny jet-black "pepper" spots (about 1 mm in diameter) are scattered over most of the pigmented surface, and are especially evident on the cheeks (Fig. 9), but may be absent in juveniles (less than 100 mm SL). The flanks posterior to the pectoral fins are marked with 5-7 bars or elongate spots, usually vertical but occasionally slightly diagonal. These extend from the basal pigmentation of the dorsum to the lower margin of the flank, which lacks basal pigmentation. An intense black spot or bar is present at the posterior axil of the pectoral fin (as in Fig. 12). Distinct bars or spots are usually absent on the flanks anterior to the pectorals. The base and distal half of the caudal may be dusky with a lighter central region, but often the entire caudal may appear uniformly dusky. The other fins are nearly devoid of pigment.

Lappets are never present. All body surfaces anterior to the anus or anal fin origin and dorsal origin are densely covered with strong close-set prickles except around the mouth (Fig. 11). Almost the entire body is covered with small, slightly imbricate dermal structures as described for *S. tyleri,* and figured for *S. greeleyi* (Fig. 8).

Sphoeroides maculatus is a large member of the genus; the largest specimen examined measured 253 mm (about 10 inches) total length.

Ecology and Distribution: Life history studies on *Sphoeroides maculatus* were published by Welsh and Breder (1922), and reproductive habits were summarized by Breder and Rosen (1966:592). The species is a spring and summer spawner which lays demersal adhesive eggs slightly less than 1 mm in diameter. These hatch in four and one-half days at 67° F.

From various seasonal records, especially Sumner, Osburn, and Cole (1911:762), Welsh and Breder (1922:261), Bigelow and Welsh (1924: 298), Hildebrand and Schroeder (1928:348), and Liem and Scott (1966: 415), it appears that *S. maculatus* summers in shallow waters along the Atlantic seacoast, but leaves these waters with cooler weather. Collections by offshore research vessels (Bullis and Thompson 1965:61) indicate that the species may spend the winter months offshore.

Sphoeroides maculatus is abundant in both estuarine and open Atlantic habitats. However, where this species is sympatric with *Sphoeroides nephelus* in northeastern Florida, it appears to be absent from bays and other estuarine waterways which are dominated by the latter species. Along the mid-Atlantic states, *Sphoeroides maculatus* is often extremely abundant, and may be considered a major pest by fishermen using cut bait. A wide variety of stomach contents (including watermelon seeds) was listed by Smith (1907:347).

Sexual maturity is attained in specimens between about 70 and 100 mm SL. Adult females average slightly longer than adult males.

The northern puffer extends from Newfoundland (Liem and Scott,

1966:415) at least as far south as Marineland, Florida (Shipp and Yerger, 1969a:426). Collections from trawlers with inexact location data indicate that offshore populations of this species may extend as far south as 27° 30' N. (near latitude of Vero Beach, Florida). This species is not present in the Gulf of Mexico (Fig. 22).

Sphoeroides maculatus is fished commercially in the Chesapeake Bay region, and is served in restaurants under the name of "Sea Squab".

Sphoeroides nephelus (Goode and Bean) Southern Puffer
(Figs. 22 and 23)

Anchisomus reticularis Richardson 1854:161 (original description, figure, Jamaica). Nomen oblitum. (see below).

Sténométope Bernierii (Bibron) Duméril 1855:278 (included in Bibron's manuscript list of species of Sténométope).

Stenometopus Bernierii (Bibron) Troschel 1856:88 (after Duméril).

Tetrodon (also *Tedrodon*) *turgidus* (not of Mitchill). Poey 1868:432 (description, Cuba). Günther 1870:285 (Lake Pontchartrain, in part). Garman 1896:93 (Bahamas).

Tetrodon turgidus nephelus. Jordan and Gilbert 1883a:306 (Pensacola).

Cirrisomus turgidus ? Goode 1879:109 (Jacksonville). Goode and Bean 1879:122 (Pensacola).

Sphaeroides spengleri (not of Bloch). Jordan 1886a:54 (Havana, Cuba). Jordan and Edwards 1886:237 (description, in part). Le Danois 1961:471 (assigns Bibron's type of *Stenometopus bernieri* (=*S. nephelus*) to *S. spengleri*).

Tetrodon nephelus. Goode and Bean 1882:412 (original description, Indian River and Pensacola, Florida). Jordan and Gilbert 1883c:966 (considered specifically distinct, removed from synonymy of *T. turgidus,* North America). Jordan 1884:146 (Key West). Jordan and Swain 1885:234 (Cedar Keys, Florida).

Sphaeroides (also *Spheroides*) *marmoratus* (not of Ranzani). Jordan and Rutter 1897:129 (Jamaica). Jordan and Evermann 1898:1733 (after Jordan and Rutter). Evermann and Marsh 1899:269 (key, description, Porto Rico). Evermann and Goldsborough 1902:158 (Cozumel Island, Yucatan). Nichols 1914:83 (description, Gulf of Mexico). Breder 1927:79 (Bahamas). Breder 1948:233 (key, description, figure). Bullis and Thompson 1965:61 (Eluthera Island, Bahamas).

Tetraodon (also *Tetrodon*) *marmoratus* (not of Ranzani). Metzelaar 1919:169 (St. Martin, West Indies). Beebe and Tee-Van 1928:264 Haiti). Nichols 1930:347 (Porto Rico).

Sphoeroides (also *Sphaeroides, Spheroides*) *nephelus.* Jordan and Evermann 1900:3178 (considered distinct from *T. spengleri*). Nichols

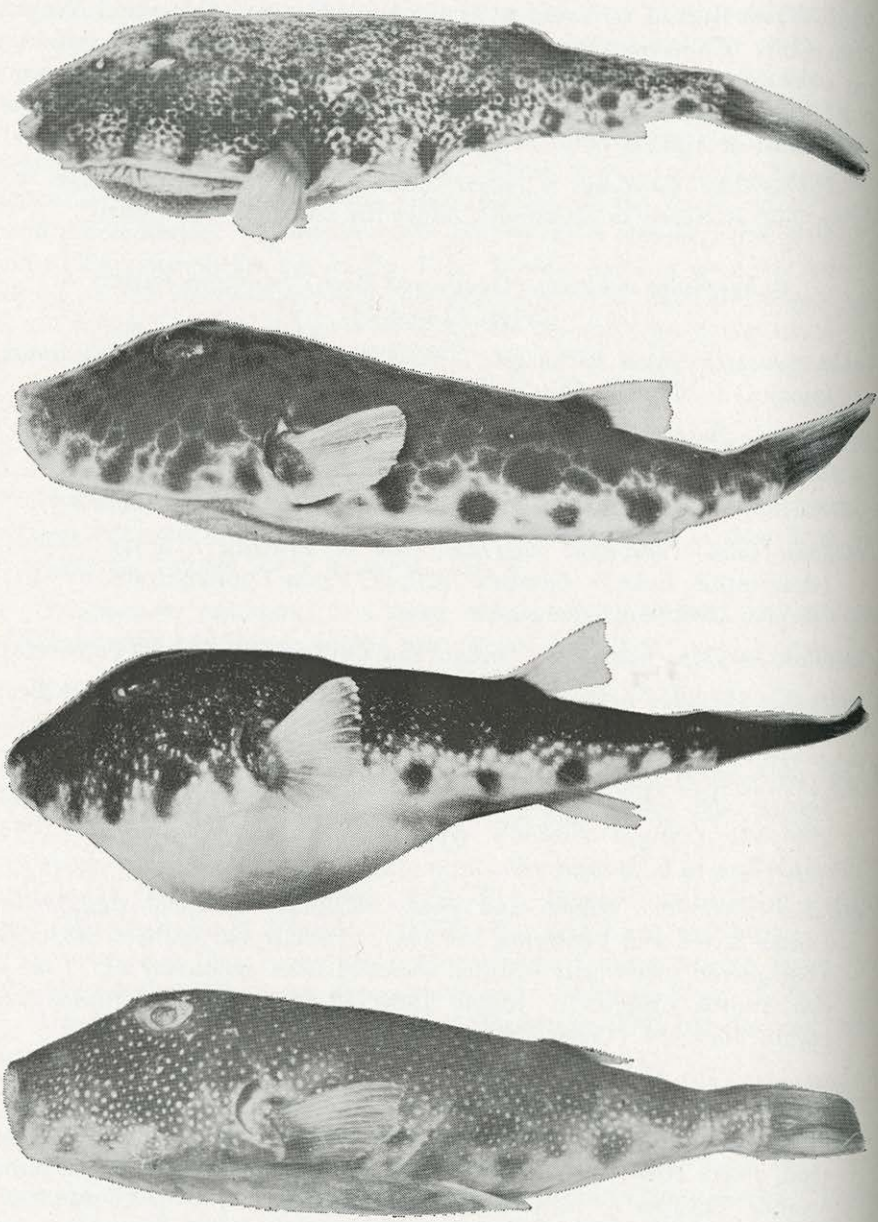

Figure 23. Variation in pigmentation in *Sphoeroides nephelus*. Upper: UMML 1366 (155 mm SL), Brevard Co., Florida. Second from top: FSU 11889 (188 mm SL), Jupiter Inlet, Florida. Third from top: UF 3750 (119 mm SL), Hernando Co., Florida. Lower: UPR 1390 (191 mm SL), La Parguera, Puerto Rico, (male with sexual dichromatic spotted pattern; spots are bright orange or red in fresh specimens).

1914:82 (description, Indian River, Florida). Jordan, Evermann and Clark 1930:498 (check list). Fraser-Brunner 1943 (listed as a "principal species" of *Sphaeroides*). Breder 1948:233 (key, description). Schultz 1949:195 (key, Florida, Caribbean). Reid 1954:71 (ecology, Cedar Key, Florida). Kilby 1955:239 (ecology, Florida Gulf Coast). Hildebrand 1955:218 (ecology, description, Gulf of Campeche, in part). Joseph and Yerger 1956:144 (Alligator Harbor, Florida). Briggs 1958:300 (Florida). Bailey et al. 1960:49 (check list, Atlantic). Springer and Woodburn 1960:89 (ecology, Tampa Bay). Tabb and Manning 1961:642 (ecology, Florida). Springer and McErlean 1962:53 (ecology, southern Florida). Herald 1965:264, 276 (figure). Böhlke and Chaplin 1968:690 (key, description, figure, Bahamas). Shipp and Yerger 1969a:425 (systematics, description, figure, Florida, Caribbean), and 1969b:477 (key, figure, considered distinct from *S. parvus*).

Sphoeroides harperi Nichols 1914:81 (original description, Cape Sable, Florida). Fowler 1940b:19 (figure, Boca Grande, Florida). Breder 1948:233 (key, description). Joseph and Yerger 1956:144 (Alligator Harbor, Florida).

Sphaeroides punctatus (not of Bloch and Schneider). Le Danois 1959:196 (systematic, description, in part).

Sphaeroides greeleyi (not of Gilbert). E. Le Danois 1961:123 (plate of *S. nephelus* labelled *S. greeleyi*).

Sphoeroides maculatus (not of Bloch and Schneider). Gunter and Hall 1963:228, 284 (ecology, Florida).

Discussion of Synonymy: The relatively recent nomenclatural history of *Sphoeroides nephelus* has been one of confusion and misidentification. The first reference which definitely applies to the species is that of Richardson (1854:161) who excellently described and figured the species as *Anchisomus reticularis.* Specimens from Jamaica, where Richardson's specimens were taken, often show a reticulate pattern of light markings on the dorsum (as in Fig. 23). Unfortunately, Richardson's description of this pattern apparently led Günther (1870:282) to mistake it for *S. testudineus,* which also displays a reticulate dorsal pattern of light markings, but one quite distinct from *S. nephelus.* Günther, therefore, erroneously considered *Anchisomus reticularis* as a junior synonym of *Tetrodon testudineus,* and the name has remained there ever since. Le Danois (1959: 197) did place the name in synonymy of her conglomerate species *S. punctatus,* which may include as many as six or more valid species. In any case, the name has not been used as a senior synonym for more than 100 years. Therefore, the International Commission on Zoological Nomenclature should be petitioned to consider the name *reticularis* as a nomen oblitum.

Bibron correctly diagnosed the specificity of *Sphoeroides nephelus,*

and designated it Sténométope Bernierii in his manuscript. This name was Latinized and published by Troschel (1856:88), but with no accompanying description, and must be considered a nomen nudum. I have examined Bibron's holotype which is deposited in the Museum National d'Histoire Naturelle, Paris, and find it to be *Sphoeroides nephelus.*

Much of the confusion regarding *Sphoeroides nephelus* in American ichthyological literature stems from David Starr Jordan's indecision as to its taxonomic status. At various times he and his coauthors confused this species with *Tetrodon turgidus* (=*Sphoeroides maculatus*) (Jordan and Gilbert, 1883a:306, considered *nephelus* as a subspecies) or with *Sphaeroides spengleri* (Jordan 1886:54, Jordan and Edwards 1886:237). The confusion with the latter species may be traced to Jordan's mistaken notion that adult *S. spengleri,* a small species, were juveniles, while the larger *S. nephelus* were thought to be adults. This is reflected by Jordan's description of young "*Tetrodon nephelus*" of Key West, Florida: ". . . caudal with two bars of blackish olive and one of white . . ." (Jordan 1884:146), a character diagnostic of *S. spengleri* from Florida. Jordan's indecision regarding this species is also reflected in two of his major works: "Synopsis of the Fishes of North America", 1883 with Charles H. Gilbert, and the "Fishes of North and Middle America", 1896-1900 with Barton W. Evermann. In the addenda of both works he elevated *S. nephelus* to the species level, after considering it as a subspecies of *T. turgidus* in the body of the earlier work, and as a junior synonym of *S. spengleri* in the latter. During the intervening years he had considered it as distinct (Jordan 1884:146, Jordan and Swain 1884:234).

Jordan and Rutter (1897:129) added further difficulties to the problem by failing to recognize the conspecificity of Caribbean populations of *S. nephelus* with Florida populations; they considered the former to be *S. marmoratus* (Ranzani). This was a strange decision in light of Jordan's awareness that *Tetrodon marmoratus* of Ranzani was a junior synonym of *S. spengleri* (Jordan and Edwards 1886:238).

Subsequent authors (see synonymies) continued to use the specific designation *marmoratus* for populations of *S. nephelus* and other species as well.

Nichols (1914:81) reviewed the American species of *Sphoeroides,* and named a form without prickles, *Spheroides harperi.* His use of such a variable character for the basis of a new species was unfortunate, since Jordan and coauthors previously had pointed out the variability of this character (Jordan 1884:146; Jordan and Swain 1884:234; Jordan and Edwards 1886:238). I have examined the holotype of *S. harperi,* and find that it is a specimen of *S. nephelus.*

Material Examined: Ninety-five series, 196 specimens.

Types: MNHN 8341 (1, 182, mounted), Martinique. Holotype of *Stenometopus Bernierii* (Bibron) Troschel. USNM 31428 (1, 156),

Indian River, Florida, lectotype of *Tetrodon nephelus* Goode and Bean designated by Shipp and Yerger (1969a:427). USNM 26570 (1, 155), Key West or Pensacola, Florida and USNM 31427 (1, 179), Indian River, Florida, paralectotypes of *Tetrodon nephelus* Goode and Bean. **North America:** UNCW uncat. (1, 133), North Carolina. FSU 11280 (1, 145), 11437 (2, 58-93), 11889 (1, 188), 12174 (1, 183), 12374 (1, 103), 12762 (1, 77), 12928 (1, 83), 13881 (3, 149-186), 13882 (4, 151-173), 13890 (1, 163), 14138 (6, 74-125), 14145(1, 117), 15020 (11, 117-162), 15576 (1, 151), GCRL 528 (1, 147), TABL (4, 155-167), UF 936 (5, 158-182), 4107 (1, 194), 11790 (1,42), UMML 571 (1, 140), 584 (1, 161), 1366 (5, 151-200), 1367 (1, 143) and USNM 133559 (2, 144-152), 133560-61 (7, 144-178), Florida, Atlantic coast. FSU 1389 (1, 143), 3665 (1, 58), 13883 (2, 71-111), 13884 (1, 116), 13885 (1, 124), 13886 (1, 128), 13887 (16, (142-214), 13889 (3, 81-108), 13891 (1, 108), 14138 (6, 74-125), 14145 (1, 117), 15021 (1, 120), 15022 (1, 153), FSU DTA-51 (1, 46), DTA-55 (2, 58-60), DTA-74 (2, 83-96), DTA-76 (1, 80), DTA-88 (6, 86-206) DTA-98 (1, 80), TABL (1, 98), (2, 77-81), (1, 74), UA 906 (1, 139), UF 2600 (3, 55-73), 2739 (6, 84-164), 3750 (1, 119), 4108 (1, 199), 9164 (1, 139), 11733 (1, 194), 11884 (2, 80-83), 15911 (1, 153), 15912 (1, 144), 15913 (1, 129), 15914 (1, 132), 15915 (1, 191), UMML 5119 (2, 71-87), 5238 (2, 85-132), 6214 (3, 79-94), 6271 (4, 57-152), 8287 (1, 184), 8922 (1, 198), 9449 (4, 78-88), 13643 (1, 61), 13928 (1, 124), 16382 (1, 190), and USNM 43574 (1, 180), Florida, Gulf Coast. GCRL 1278 (1, 160), S. of Horn Island, Mississippi. BMNH (1, 145), New Orleans, Lake Pontchartrain, Louisiana. **Central America:** IMST 620 (1, 157), Campeche, Mexico. USNM 192239 (1, 152), eastern Yucatan. GCRL 3206 (1, 54), 9984 (1, 116), Colon, Panama. **Caribbean Islands:** LACM 5958 (2, 24-28), 5959 (1, 23), 5960 (15, 70-86), USNM 38554 (1, 111), Jamaica. UF 3506 (1, 22), Bahama Islands. ANSP 72566 (1, 49), New Providence, Bahamas. ANSP 94255 (1, 166), Hatchet Bay, Bahamas. ANSP 94256 (1, 154), Nassau Harbor, Bahamas. ANSP 94258 (1, 170), Hog Island, Bahamas. FSU 13880 (1, 155), Grand Bahama Island. UPR 1390 (4, 191-220), 2383 (1, 215), 2951 (1, 190), Puerto Rico. ANSP 690 (1, 138), St. Martin's Island.

Diagnosis: *Sphoeroides nephelus* is a richly pigmented species, recognized by the presence of discrete light reticulations or vermiculations over the entire pigmented surface. Spots bound the ventrolateral body angle; the axil spot is most intense (Fig. 12). In addition, it has a long snout, no lappets, and a narrow, often concave interorbit. It lacks the tiny jet black spots of *S. maculatus* and the coarse, light, dorsal arches and circular markings of *S. testudineus.*

General Description (Tables 2-4, 9): Head of adults 2.6 to 2.8 in SL, just slightly longer in subadults. Snout long, 1.6 to 1.8 in head, longest in adults. Eye 4 to 7 in head, usually about 5.0 to 5.5. Least bony interorbit usually concave, narrow, 4 to 8 in snout, usually about 6,

and about 10 in head. Dorsal shorter than snout, usually contained 1.1 to 1.3 in snout, and 2.2 in head. Anal shorter, usually 1.4 to 1.5 in snout, and about 2.5 in head. Dorsal fin origin slightly anterior to anus, well anterior to anal fin origin. Caudal slightly rounded, moderate, but equal to or a little less (1.0-1.3) than snout, and about 2 in head, except in juveniles in which the caudal may be slightly longer than the snout. Pectoral fins moderate, longest ray about 1.2 to 1.4 in snout, about 2.2 in head. Dorsal rays 8, anal rays 7, pectoral rays usually 14 or 15 (rarely 13). Caudal rays 11, with the first (and rarely second) upper and two lower rays unbranched.

Pigmentation is restricted to the dorsolateral surfaces. Basal pigmentation is deep brown or gray, and extends ventrally to the ventrolateral body angle. Thin discrete light (pale green or blue in fresh specimens) specks, vermiculations, or reticulations characterize the pigmented surfaces. These patterns are most distinct on the upper flanks, less distinct or lacking on the dorsum. Large dark spots are present on the pigmented surfaces, and are often enclosed by the light reticulations. Laterally and posterior to the pectoral fin these spots bound the ventral margin of the pigmented surface; the spot at the axil of the pectoral fin is most intense (as in Fig. 12). Anterior to this fin the spots may be replaced by vague oblique bars. A dark bar extends between the orbits. Sexually mature, ripe males sometimes are covered with brilliant red or orange spots about 1 mm in diameter. These appear white in preserved specimens (Fig. 23). The caudal is typically dusky at its base and distal half, but rarely may exhibit dark, vague proximal and distal bands. The other fins are nearly devoid or pigment.

Lappets are absent. The presence of prickles and their extent of coverage is variable (see geographic variation below). Some specimens are heavily prickled, with all areas anterior to the dorsal fin and anus (except lips) covered (Fig. 11). Other specimens may lack prickles along the flanks, or parts of the dorsum and belly, while still others may lack prickles entirely. Almost the entire body is covered with small, slightly imbricate dermal structures as described for *S. tyleri,* and figured for *S. greeleyi* (Fig. 8).

Sphoeroides nephelus is a large member of the genus; the largest specimen examined measured 258 mm (about 10 inches) total length.

Geographic Variation: Only *Sphoeroides greeleyi* exceeds *S. nephelus* in the extent and degree of geographic variation. Three relatively discrete populations exist; however, clinal gradations between them are evident.

Along the northeast Florida coast from Jacksonville south to near Miami, *Sphoeroides nephelus* is characterized by a relatively broad (about 12.3% of head length, 21% of snout length) slightly concave bony interorbit, by heavy prickle coverage, and by a high pectoral fin ray count

(M=14.4, N=32). In addition, the basal body pigmentation is extensively vermiculated with distinct light marking (Fig. 23).

From the west and northwest Florida coast, *Sphoeroides nephelus* possesses a distinctly concave bony interorbit of moderate width (about 10.4% of head length, 18% of snout length). Prickle coverage may be heavy, but often prickles are restricted to small areas of the back and/or belly, or they may be totally lacking, a condition especially common along the southeast Florida coast. This population averages fewer pectoral rays (M=14, N=47). Basal body pigmentation may be heavily vermiculated with light markings, or these may be reduced to small light spots or crescents which are less evident (Fig. 23).

Caribbean and Central American populations exhibit an extremely narrow (about 8.6% of head length, 14% of snout length), concave bony interorbit. Prickle coverage is variable, but individuals devoid of prickles are rare. Each discrete, light marking on the basal body pigmentation may include a dark spot. In this region, ripe males may be covered with brilliant red or orange (light in preservative) small spots (Fig. 23).

The three populations just described seem to converge in extreme southeast Florida and in the Florida Keys. From this region specimens may exhibit any combination of the characters described above, and this area appears to be the center of gene flow between populations.

Ecology and Distribution: *Sphoeroides nephelus* is a shallow water species, restricted in some areas to estuarine bays, canals, and sounds. It is especially abundant in such habitats along the central/east Florida coast where it is considered an ever-present pest by bait fishermen. Gunter and Hall (1963:248) reported it (as *S. maculatus*) from salinities of 22.8 to 27.4 o/oo and temperatures of 25.6-28.3 °C from the estuary at St. Lucie, Florida. Along more northern areas of that coast, juveniles may be collected with juvenile *S. maculatus* in estuaries, but adults of *S. maculatus* have been taken only in open Atlantic waters in these areas of sympatry. *Sphoeroides nephelus* is also common in estuaries of the west and northwest Florida coasts, but its capture in this area from waters of full ocean salinity is rare. Tabb and Manning (1961:642) took this species from Florida Bay in salinities from 10 o/oo to 40 o/oo and temperatures of 19-28 °C. Collections indicate that it is not especially common in Caribbean habitats. In more temperate regions of its range *S. nephelus* spawns from spring through fall. Ripe adults from the Caribbean and southern Florida have been taken at all seasons.

Sphoeroides nephelus occurs from northeast Florida (with stragglers north to North Carolina) southward throughout the Caribbean to Martinique. It also occurs in the Gulf of Mexico commonly as far north and west as Pensacola, and in the southern Gulf in Yucatan. Stragglers may reach New Orleans, but it is absent in the western Gulf. Records from Central America are rare, but it has been taken from the Caribbean coast of Yucatan and Panama (Fig. 22).

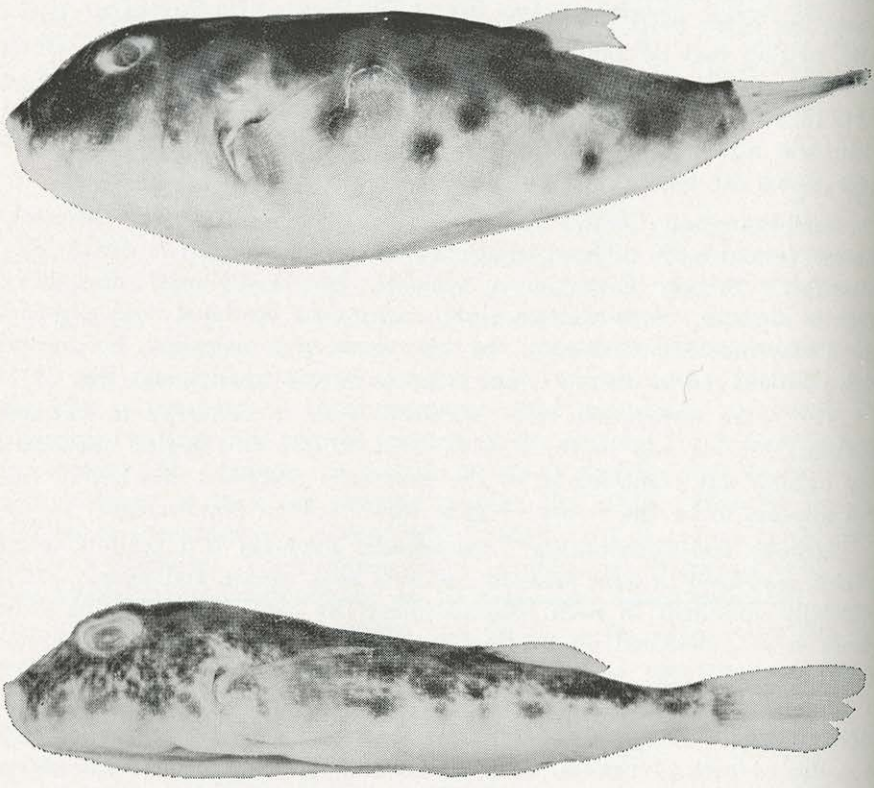

Figure 24. Upper: *Sphoeroides georgemilleri* ANSP 110218 (92 mm SL), holotype, off Colombia. Lower: *S. parvus* FSU 15365 (75 mm SL), paratype, Mobile Bay, Alabama.

Sphoeroides georgemilleri Shipp Plaincheek Puffer
(Figs. 24 and 25)

Sphoeroides georgemilleri Shipp 1972:132 (original description, Colombia).

Discussion of Synonymy: Except for the original description of the species, no reference has been made in the literature to this species.

Material Examined: Four series, 9 specimens.

Holotype: ANSP 110218 (1, 91.8) 08° 59 N, 76° 27' W., 12 fathoms, off Colombia. **Paratypes:** UMML 22262 (2, 53-54), 08° 48'-46.8' N., 76° 39'-42.8' W. UMML 30327 (1, 56), 08° 21.6' N., 76° 47.6' W. ANSP 117319, taken with holotype, (5, 79-95). All off Colombia.

Diagnosis: *Sphoeroides georgemilleri* is a species with uniform basal pigmentation, and scattered dark spots and blotches. The cheeks show primarily basal pigmentation. The axil spot is not intense; dorsum and flanks lack discrete pattern of markings. Prickles on dorsum extend posteriorly only to the level of the posterior margin of the pectoral fin. Scale-like dermal development is evident on the flanks; lappets are absent.

General Description (Tables 2-4, 9): Head 2.6 to 3 in SL, longer in subadults. Snout 1.5 to 2.0 in head, longest in larger specimens. Eye large, 4.2 to 5.3 in head. Least bony interorbit very slightly concave, broad 2.4 to 2.9 in snout, about 3.5 in head. Dorsal nearly equal to or slightly shorter than snout, contained 1.0 to 1.3 in snout, about 1.8 in head. Dorsal fin origin directly opposite anus, slightly anterior to anal fin origin. Caudal slightly rounded, 0.7 to 1.1 in snout, about 1.4 in head. Pectoral fins moderate, longest ray (exposed length) 1.2 to 1.5 in snout, about 2.2 in head. Dorsal rays 8 (rarely 9), anal rays 7; pectoral rays usually 16 (rarely 15 or 17); caudal rays 11, with the first upper and two lower rays unbranched.

Pigmentation of preserved specimens is restricted to the dorsolateral surfaces. Basal pigmentation is light gray or brown, and extends ventrally to a few mm above the ventrolateral body angle, where it fades and finally disappears just above or at this angle. Dark blotches and spots are present on the pigmented regions, and may form patterns of narrow transverse saddles or bars. Such a pattern is especially evident on the dorsum between the pectoral fin bases. A few blotches are present on the flanks, but the cheeks usually lack distinct markings. The spot in the axil of pectoral fin is not especially distinct. A dark, irregular bar extends between the orbits. The caudal usually exhibits a narrow basal bar and a broad distal bar, both of which vary in intensity and distinctness. The base of the dorsal fin is pigmented; other fins are nearly devoid of pigment.

Lappets are absent. Scale-like dermal development posterior to the pectoral fins is very distinctive, and comparable to the condition in *Sphoeroides greeleyi* (see Fig. 8). Prickles are absent laterally; on the dorsum

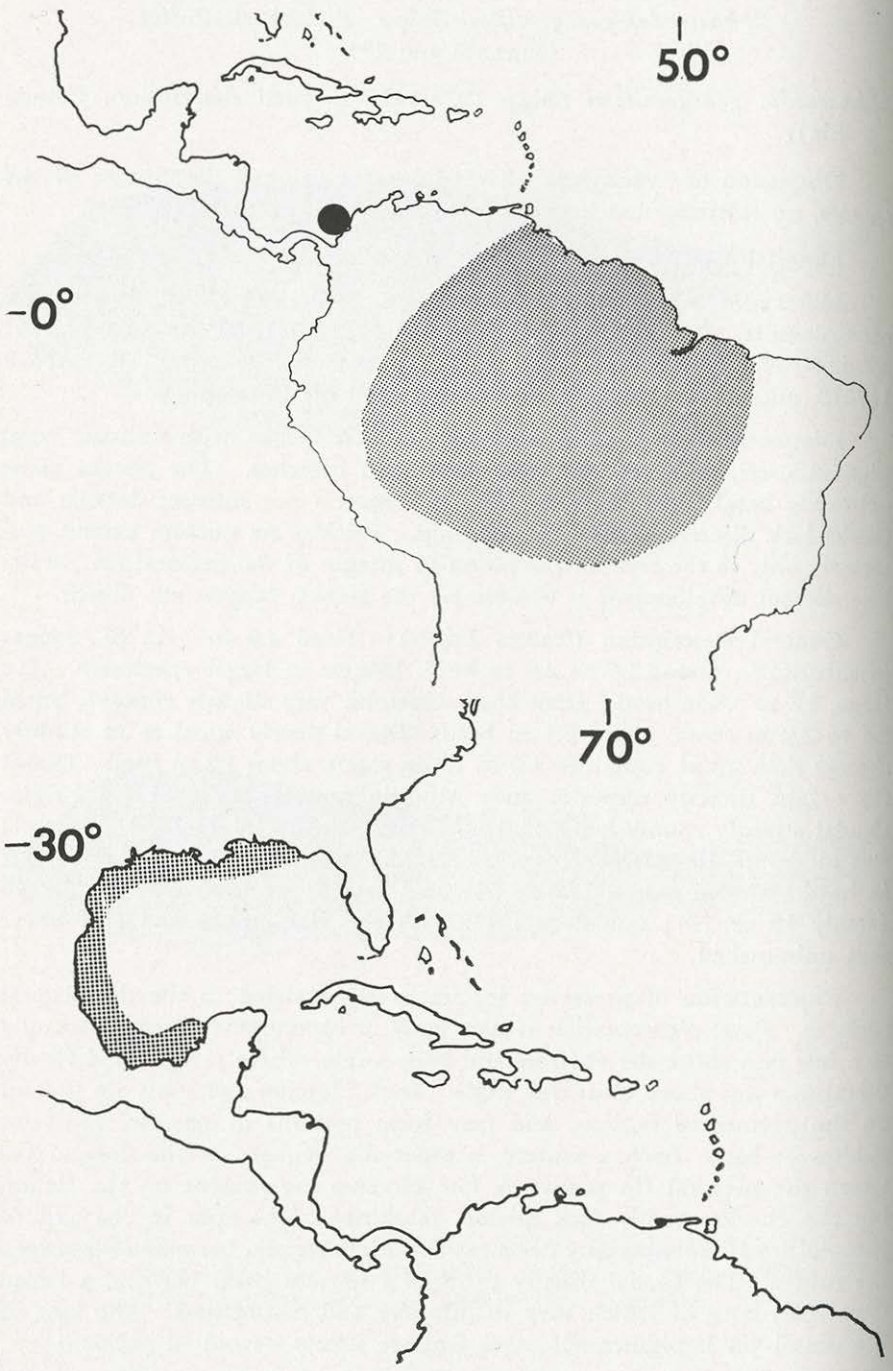

Figure 25. Upper: Distribution of *Sphoeroides georgemilleri* (black spot), and *Colomesus asellus*. Lower: Distribution of *S. parvus*.

they extend from the nape posteriorly to the level of the posterior margin of pectoral fin. On the belly they extend from chin posteriorly to a point several mm anterior to the anus, where they terminate abruptly.

The largest specimens examined were 120 mm (about 5 inches) total length.

Sphoeroides parvus Shipp and Yerger Least Puffer
(Figs. 24 and 25)

Tetrodon turgidus (not of Mitchill). Günther 1870:285 (Lake Pontchartrain, in part).

Tetrodon turgidus nephelus (not of Goode and Bean). Jordan and Gilbert 1883a:306 (Galveston and Pensacola, in part).

Sphoeroides (also *Sphaeroides*) *nephelus.* Burkenroad 1931:22 (sound production, Louisiana). Baughman 1950:256 (Texas). Hildebrand 1954:320 (description, ecology, Louisiana, Texas, Gulf of Campeche). Hildebrand 1955:218 (description, ecology, Gulf of Campeche). Reid 1956:296 (ecology, Texas). Boschung 1957:567 (description, ecology, Mobile Bay, Alabama). Reid 1957:203 (ecology, Texas). Hoese 1958:347 (check list, Texas). McFarland 1963:100 (ecology, Mustang Island, Texas). Miller 1965:103 (ecology, Port Aransas, Texas). Parker 1965:218 (Galveston, Texas). Roithmayr 1965:23 (north-central Gulf of Mexico). Dawson 1966:179 (Grand Isle, Louisiana). Franks et al. 1972:126 (ecology, north-central Gulf of Mexico).

? *Sphoeroides spengleri* (not of Bloch). Fowler 1931b:50 (Port Aransas, Texas).

Sphoeroides marmoratus (not of Ranzani). Gunter 1945:84 (description, ecology, Texas). Baughman 1950:256 (after Gunter).

Sphoeroides eulepidotus (not of Metzelaar). Schultz 1949:196 (Texas in part).

Sphoeroides sp. Reid 1955:331, 449 (ecology, East Bay, Texas).

Sphoeroides parvus Shipp and Yerger 1969b:477 (original description, synonymy, key, figures, ecology; Apalachicola Bay, Florida, to Gulf of Campeche). Franks et al. 1972:43 (component of nekton, north-central Gulf of Mexico).

Discussion of Synonymy: *Sphoeroides parvus* has been known by several names, but most commonly confused with the closely related *S. nephelus.* The first literature record definitely attributable to *S. parvus* was that by Günther (1870:285). In his "Catalogue of Fishes of the British Museum", he listed three specimens from Lake Pontchartrain as examples of *Tetrodon turgidus* (=*S. maculatus*). I have examined these and find that the largest specimen is *S. nephelus,* the westernmost example I have found of this species. The two smaller individuals are typical specimens of *S. parvus.*

Jordan and Gilbert (1883a:306) considered material now known as *S. nephelus* and *S. parvus* to be subspecies of *Tetrodon turgidus* (=*S. maculatus*), and noted that they were very abundant around Pensacola and Galveston; it is clearly one or both of these species to which Jordan and Gilbert referred. Pensacola is an area of sympatry of *S. nephelus* and *S. parvus* (though *S. nephelus* is much more common) and it is likely that *S. nephelus* or even both species were seen by these authors at that locality. Juveniles of *S. nephelus* are superficially quite similar to *S. parvus,* and consideration of the two species as one would not be surprising, even when collected together. Only *S. parvus* is abundant at Galveston.

Most twentieth century references to the common puffer of the Texas coast identified this species as *S. nephelus.* However, Gunter's (1945:84) treatise on the fishes of Texas identified this form as *Sphoeroides marmoratus* of Ranzani. As discussed earlier (see synonymy of *S. spengleri*), Ranzani's description of *Tetraodon marmoratus* refers to *Sphoeroides spengleri.*

Schultz (1949:196) assigned to *Sphoeroides eulepidatus* those specimens with scale-like dermal development, thus including in this species certain specimens in the U. S. National Museum from Texas waters. *Sphoeroides parvus* (as well as several other species) possess such a character, and I have examined USNM series (not the same as Schultz studied) which were identified as *S. eulepidotus,* and find them to be *S. parvus. S. eulepidotus* is a junior synonym of *S. greeleyi,* a species which does not reach Texas; therefore it appears evident that Schultz's description of *S. eulepidotus* referred in part to *S. parvus.*

Hildebrand (1955:218) called attention to two "types" of *S. nephelus* from Campeche. His specimens have been examined and found to represent *S. nephelus* and *S. parvus.*

Material Examined: Thirty-eight series, 446 specimens.

Holotoype: USNM 203248 (1, 79.7), Mobile Bay, Alabama. **Paratypes:** UMML 2618 (1, 62), Apalachicola, Florida. UF 4437 (8, 54-69), Choctawhatchee Bay, Florida. UF 2731 (2, 52-57), Pensacola and TABL (1, 53), lower Pensacola Bay, Florida. UA 62 (5, 47-64), Gulf Shores, Alabama. FSU 15364 (35, 32-54) and 15365, taken with holotype, (176, 21-90), Mobile Bay. UA 296 (15, 48-86), UA 397 (5, 46-97), UA 1290 (17, 47-79), all from Mississippi Sound, Alabama. UA 625 (22, 30-58), Mississippi Sound, Mississippi. TU 9381 (1, 51), Lake Pontchartrain, Louisiana. TU 22573 (14, 41-67), off Grand Terre, Louisiana. ANSP 97647 (51, 42-75), Barataria Bay, Louisiana. TU 19038 (2, 80-90), Cameron, Louisiana. NMFS-G Gus 1 E 25 (1, 56), 29° 01' N., 95° 05' W. NMFS-G Gus 3 W 13 (1, 62), 28° 19' N., 96° 21' W. ANSP 98279 (2, 54-56), 28° 17.5' N., 93° 57.5' W. NMFS-G Gus 4 W 1 (3, 58-62), 29° 01' N., 95° 05' W. NMFS-G Gus 1 W 11 (2, 51-87), 27° 42' N., 97° 05' W. ANSP 98275 (2, 50-55), 26° 18' N., 97° 11' W. IMST 624

(1, 118), Aransas Bay, Texas. IMST 614 (3, 62-71), off Pts. Frontera, Mexico. IMST 619 (8, 63-75), Campeche to Champoton, Mexico. IMST 622 (4, 80-85), W. of Campeche, Mexico. **Other specimens examined:** FSU 14152 (3, 51-52), Santa Rosa Sound, Pensacola, Florida. UA 286 (1, 104), Mobile Bay, Alabama. GCRL 1284 (1, 51), S. of Horn Island, Mississippi. LCFU (48, 28-65), USNM 155990 (1, 70), and GCRL 311 (1, 51), Louisiana. USNM 73580 (1, 64), 118648 (1, 88), 155989 (1, 111), 155992 (1, 111), 156492 (3, 63-86), ANSP 98263 (1, 71), Texas.

Diagnosis: *Sphoeroides parvus* is a small puffer, recognized by its short snout, broad flat interorbit, and nondescript pigmentation pattern. In addition, this species lacks lappets, and the spot at the axil of the pectoral fin, if present, is not more deeply pigmented than other lateral markings. Such a spot is always present and distinctive in the sympatric *S. nephelus* (Fig. 12). *Sphoeroides parvus* lacks the distinctive dorsal pattern of coarse, light arches and circular markings which is found in *S. testudineus,* a sympatric species in the southern Gulf of Mexico (Fig. 10).

General Description (Tables 2-4, 9): Head of adults 2.7 to 3.1 in SL, slightly longer in subadults. Snout 1.8 to 2.2 in head, longest in adults. Eye 3.5 to 7 in head, usually about 4.2 to 4.7. Least bony interorbit broad, flat, 2.6 to 3.9 in snout, usually about 3.4, about 7 in head. Dorsal rarely shorter than snout, usually 0.8 to 1.0 in snout, about 1.9 in head. Anal shorter, usually 1 to 1.2 in snout, about 2.2 in head. Dorsal fin origin directly over anus, slightly anterior to anal fin origin. Caudal slightly round, almost always longer than snout, usually 0.8 to 1.0 in snout, about 1.8 in head. Pectoral fins moderately long, longest ray 0.9 to 1.1 in snout length, about 2 in head. Dorsal rays usually 8 (rarely 9), anal 7 (rarely 6), pectoral rays 14 or 15 (rarely 13 or 16). Caudal rays 11, with the first, and sometimes the second, upper and two lower rays unbranched.

Pigmentation of preserved specimens is restricted to the dorsolateral surfaces. Basal pigmentation is brown or gray, lighter on the flanks, and fades just above the ventrolateral body angle. The basal pigmentation is characterized by light, indiscrete specks or vermiculations (pale green or blue in fresh specimens). A few small scattered spots are also present dorsally; laterally, larger spots or blotches tend to border the poorly defined ventral edge of the basal pigmentation. Sometimes a blotch is present in the pectoral fin axil, but rarely is it more intense than other lateral spots or blotches. A vague dark bar extends between the orbits. The caudal is dusky, with pigment sometimes concentrated near the base and distal half; other fins are nearly devoid of pigment.

Lappets are absent. Prickles are always present and extremely close set. Dorsally, they extend from immediately anterior to the nasal papillae to the dorsal fin origin; laterally, they are usually present on the greater portion of the cheek and sides to near the level of the dorsal fin. On the ventral surface, prickles extend from chin to near the anus, occasionally

ending abruptly about the level of the posterior pectoral margin. Almost the entire body is covered with small, imbricate dermal structures as described for *Sphoeroides tyleri,* and figured for *S. greeleyi* (Fig. 8).

The largest specimen examined was 148 mm (about 5.5 inches) total length.

Ecology and Distribution: *Sphoeroides parvus* is a shallow water species restricted to turbid waters of the western Gulf of Mexico; it is abundant in many areas. Reid (1957:203) listed it as the ninth most common species among those captured by trawl in Galveston Bay. Although it frequents estuaries and has been taken at salinities as low as 4.1 o/oo, Gunter (1945:84) stated that it is rare at less than 10 o/oo. My collection data and material examined indicate that juveniles are much more abundant than adults in low salinity water. It occurs in water as deep as 20 fathoms (Dawson 1966:179), but is more common in shallow habitats. This species is a spring and summer spawner; males mature at about 50 to 60 mm SL, females at about 60 to 70 mm SL.

Sphoeroides nephelus and *Lagocephalus laevigatus* are the only tetraodontids known to have been taken in collections with *S. parvus* in the northern Gulf. Although, *S. spengleri, S. dorsalis,* and *S. pachygaster* are also geographically sympatric in that region, they are usually found in more offshore or deeper water habitats. *Sphoeroides parvus* has been taken with a number of tetraodontids from waters off Campeche, Mexico.

Sphoeroides parvus ranges from Apalachicola, Florida throughout coastal areas of the western Gulf of Mexico, to the Campeche Banks of Mexico (Fig. 25). It is uncommon along the Florida segment of that coastline; in this region of clear water, the dominant puffer is *S. nephelus.* However, from Mobile Bay westward and around the Gulf of Mexico to Yucatan, *S. parvus* is the abundant inshore puffer. It is sympatric with *S. nephelus* along the Campeche Banks, and is the more common species (Hildebrand 1955:218).

GENUS *COLOMESUS*

Colomesus is a little known genus of Tetraodontidae comprised of two species. The systematics of this genus have been thoroughly reviewed by Tyler (1964). My analysis of his findings is in almost complete agreement in respect to the systematics of *Colomesus.* Certain problems, results, and tentative conclusions which Tyler presented in his paper on other aspects of teraodontid systematics have been discussed above.

For reasons of completeness in this regional treatment of the family, I have modified Tyler's data on *Colomesus* to conform to present format, and added significant data obtained from additional material. I take no credit for the majority of the bibliographic examination presented here.

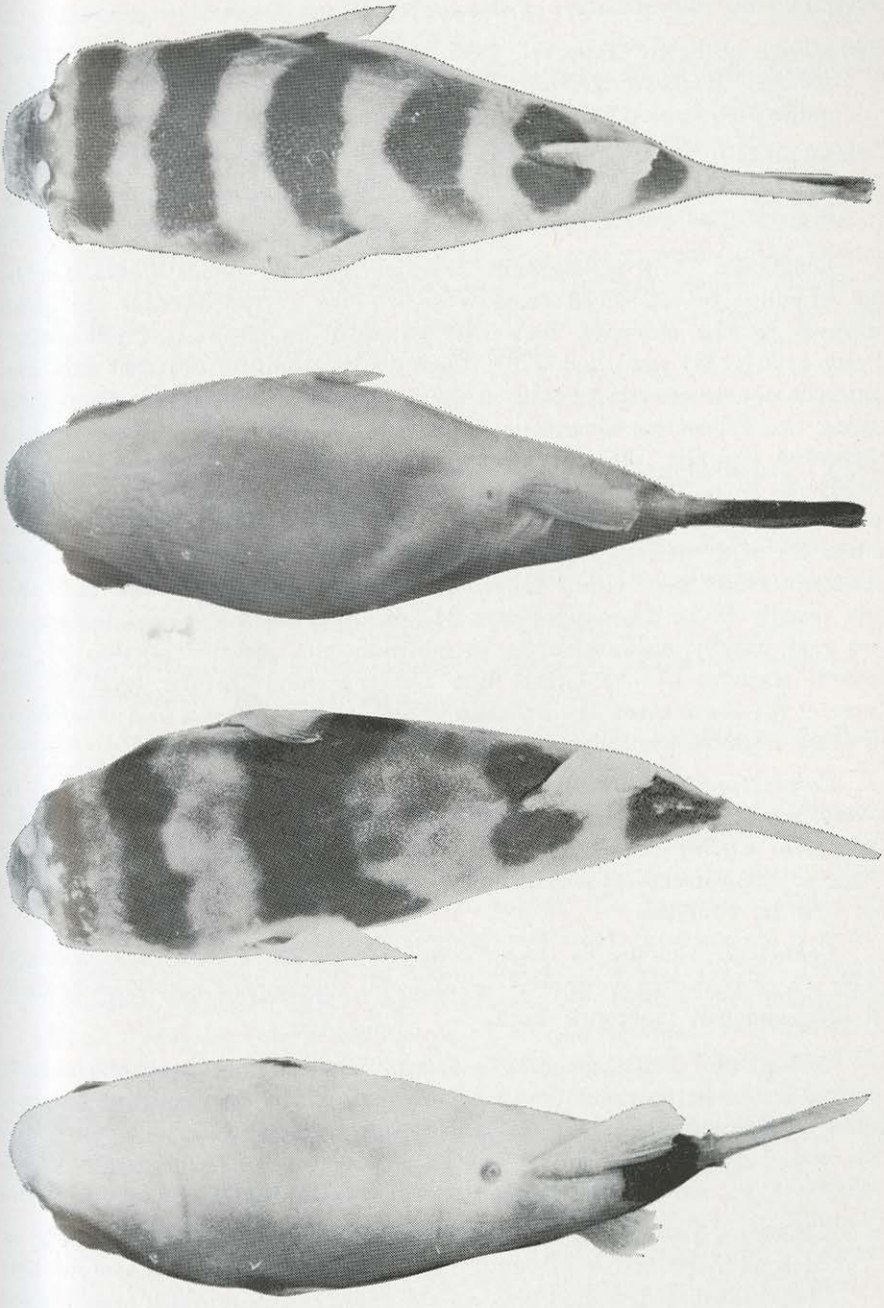

Figure 26. Dorsal and ventral views of two species of *Colomesus,* demonstrating interspecific pigmentation variation Upper two: *Colomesus psittacus* RMNH 21534, Surinam. Lower two: *Colomesus asellus* FSU 17521, Peru.

Colomesus Gill

Batrachops (Bibron) Troschel, 1856, p. 88 (after Duméril 1855). Type-species: *Tetrodon psittacus* Bloch and Schneider, 1801, by monotypy, name preoccupied by *Batrachops* Heckel, 1840:432, a cichlid.

Colomesus Gill, 1884, p. 422 (substitute name for *Batrachops* Bibron, therefore taking the same type-species, *Tetrodon psittacus* Bloch and Schneider, 1801, as well as by Gill's designation).

Diagnosis: Gill (1884:422) characterized the genus *Colomesus* by the presence of narrowed frontals which are excluded from the orbit margins by the elongate, forwardly extended postfrontals (sphenotics). Tyler (1964:128) qualified Gill's diagnosis by pointing out that this condition is not necessarily present in specimens less than 100 mm SL. Tyler added the following diagnostic features: "Anterior ends of sphenotics expanded laterally into slightly posteriorly directed wings. Vertebrae usually 8 + 11 = 19. Lower lateral line present from before anal fin to base of caudal fin; separate from upper lateral line. Olfactory organ a low sac with nostrils laterally and anteromedially; inner surface of sac plain anteriorly but with a horizontal fold posteriorly. Dorsal and anal rays usually 10 or 11; caudal rays 11, the uppermost ray and lowermost two rays usually unbranched." In addition, the anterior portion of the ventral segment of the lateral line system extends to the level of the pectoral fin and is more distinct than in either *Lagocephalus* or *Sphoeroides*. In other respects, the lateral line system is as in *Sphoeroides*.

Colomesus psittacus possesses scale-like dermal structures as found in several species of *Sphoeroides* (see description of *Sphoeroides tyleri*) and *Colomesus asellus* possesses dermal lappets, but it is not clear whether either of these structures is homologous to similar structures in *Sphoeroides*. All fins are rounded.

Colomesus is closest to *Sphoeroides*, and may share a common ancestral stock which branched from the *Lagocephalus* ancestor, or may have branched independently from this stock.

Ecology and Distribution: *Colomesus* inhabits both fresh and marine shallow waters of northern South America. It is the only western Atlantic genus of Tetraodontidae with a fresh water species.

KEY TO SPECIES OF *COLOMESUS*

A. Pectoral rays 17 to 19 (usually 18) (Table 2). No lappets or dermal flaps across the chin. Dorsum with 6 dark transverse bars (excluding a darkened area on the snout), and no dark spot on the underside of the caudal peduncle (Fig. 26)
..... *Colomesus psittacus* (Bloch and Schneider)

AA. Pectoral rays 13 to 16 (usually 14 or 15). Lappets or dermal flaps present across the chin. Dorsum with 5 dark transverse bars (ex-

cluding a darkened area on the snout). A dark spot on underside of the caudal peduncle (Fig. 26)

..... *Colomesus asellus* (Müller and Troschel)

Colomesus psittaus (Bloch and Schneider) Corrotucho
(Figs. 27 and 28)

Tetrodon psittacus Bloch and Schneider 1801:505 (original description, figure, "mari Malabarico" = Bay of Bengal or eastern Indian Ocean, an error). Günther 1870:286 (Guianas, Surinam, Brazil, in part). Boulenger 1897:298 (Marajo, Brazil, in part). Puyo 1949:248 (description, figure, French Guiana, in part).

? *Tetrodon fasciatus* Bloch and Schneider 1801:508 (original description, after Seba).

Tetrodon semispinosus Freminville 1813:253 (original description, figure, "Saint Dominique" = Hispaniola, probably an error).

Chelichthyes psittaus. Müller and Troschel in Richard Schomburgk, 1848:641 (description, differentiated from *C. asellus,* British Guiana).

Chelonodon psittaus. Rüppell, 1852:35 (after Bloch).

Batrachops psittacus (Bibron) Duméril 1855:280 (type of monotypic genus, used in vernacular sense).

Batrachops psittacus (Bibron) Troschel 1856:88 (after Duméril). Hollard 1857:322 (figure of skull).

Colomesus psittacus. Gill 1884:422 (type-species of monotypic genus). Jordan and Edwards 1886:244 (synonymy, Guiana, Brazil, in part). Eigenmann and Eigenmann 1892:73 (South America, in part). Gill 1892:714 (fig. of skull, in part). Jordan and Evermann 1898:1740 (South America, in part). Eigenmann 1905:484 (S. America, in part). Ribeiro 1915:page 17 of Tetraodontidae section and 1918:68 (Brazil, in part). Fowler 1931a: 405 (Trinidad). Jordan, Evermann and Clark 1930:500 (check list, in part). Fraser-Brunner 1943:12 (osteology, in part). Santos 1954:159 (Brazil, in part). Price 1955:410 (Trinidad). Le Danois 1959:212 (systematics, in part). Boeseman 1960:143 (Trinidad) Y. Le Danois 1961:473 (considers type-specimens of *Tetrodon semispinosus* Freminville to be *Colomesus psittacus* and type-species of the genus *Batrachops* of Bibron to be *Colomesus psittacus*). Durand 1961:43 (ecology, Guianas). Lowe (McConnell) 1962:697 (Guianas). Tyler 1964:119 (systematics, figures). Cervigon 1965:67 (Venezuela) and 1966:836 (ecology, figures, Venezuela). Gines and Cervigon 1968:38 (ecology, Guianas and Surinam).

Tetrodon (*Cheilichthys*) *psittacus.* Metzelaar 1919:171 (synonymy, description).

Discussion of Synonymy: Although the two recognized species of

Colomesus were described in the first half of the nineteenth century (*psittacus* in 1801, *asellus* in 1848), they have not generally been considered distinct until the review of the genus by Tyler (1964). Müller and Troschel (1848b:641) apparently recognized the distinctive characters of *asellus* when they originally described this species, but they did not stress diagnostic differences between the species (Tyler 1964:120). Subsequently Steindachner (1861:141) labelled his diagnostic figure of *Colomesus asellus* as *Chelichthyes psittacus,* an error standardized in Günther's Catalogue of Fishes of the British Museum (1870:286). Thus, for nearly a hundred years the genus was considered monotypic, and many references which may refer to both species occur in the literature. These are included under synonymy of both species with the notation "in part". Where descriptions or significant ecological data are present and are diagnostic of a species, the reference is limited to the synonymy of that species.

The species was given a diagnostic description and figured by Bloch and Schneider (1801:505, Fig. 95). The type-locality "mari Malabarico" (=Indian Ocean) is obviously an error.

Also included questionably in the synonymy of this species by Tyler (1964:121) was *Tetrodon semispinosus* of Freminville. I have examined the types of this nominal species in the Museum National d'Histoire Naturelle, Paris and find them to be juvenile *T. psittacus,* thus removing doubt as to the status of *T. semispinosus* as a junior synonym. Tyler pointed out that the type-locality ("Saint Dominque" = Hispaniola) of this species is probably an error, as it is outside the known range of the species.

The two species of *Colomesus* have been taken together from Marajo Island, Amazon River mouth, Brazil. Therefore, Boulenger's note (1897) of *T. psittacus* from this locality is included questionably under the synonymy of both species.

Material Examined: Tyler (1964:145) examined 35 specimens, 12.4 to 289.2 mm SL from Trinidad, Venezuela, British Guiana, and Surinam (and four specimens with no locality data). In addition, I have examined 21 series, of 118 specimens which are listed below. Tables and descriptions are drawn from both sources.

Types: MNHN A 5257 (2, 41.2-45.1) ? "Saint Dominique" (=Hispaniola) paratypes of *Tetrodon semispinosus* Freminville. MNHN B 1569 (1, 268), "Coast of Guyana", "Genotype de Batrachops" of Bibron. **South America:** EIMM F.C. 984 (1, 55), Golfo de Paria, Venezuela. UMML 12176 (2, 100-116), RMNH 915 (1, 170), 7340 (5, 44-70), 9859 (1, 223), 16345-16347 (5, 26-60), 18118 (7, 43-59), 21534 (1, 60), 24779 (2, 36-38), uncat. (5, 20-21), (2, 128-212), (1,196), (1, 128), (66, 14-55), (1, 175), Surinam. BMNH (13, 11-52), Marajo Island. MZUSP 7665 (1, 128), Aracaju, Sergipe, Brazil.

Diagnosis: *Colomesus psittacus* is easily distinguished from other

Atlantic puffers by the six broad transdorsal bars (Fig. 26). In addition, it has 11 dorsal (rarely 10 or 12) and 11 anal (sometimes 10, rarely 12) rays; no lappets are present. It lacks the black blotch on the ventral surface of the caudal peduncle which is found in the only known congeneric species, *C. asellus.*

General Description (Tables 2-4, 10): Head about 2.6 in SL, only slightly longer in subadults. Snout short, 2.3 to 2.6 in head, shorter in subadults. Eye small, about 7 to 8 in head. Least bony interorbit flat to very slightly convex, very broad, occasionally broader than length of snout, usually 0.9 to 1.5 in snout, about 2.8 in head. Dorsal longer than snout, usually 0.7 to 0.9 in snout and about 1.9 in head; anal about equal to dorsal in length. Dorsal fin origin directly over anus, well anterior to anal fin origin. Caudal slightly rounded, long, 0.6 to 0.7 in snout, about 1.5 in head. Pectoral moderate in length, usually 0.9 to 1.2 in snout, about 2.4 in head. Dorsal rays usually 11, rarely 10 or 12, anal rays 10 or 11, with the first upper and two lower rays unbranched.

Basal pigmentation of upper surfaces is light brown or gray, with six dark, prominent, uniform, transverse bars (Fig. 26). The first extends between the orbits; the second, third and fourth extend across the middle of the back; the fifth across the dorsal fin base, and the sixth across the caudal peduncle. The light interspaces are about equal to the width of the bars. Occasionally individuals may display darkened areas within these interspaces. A darkened area, reminiscent of still another bar is present on the snout, and a slightly darkened area is often present posterolateral to the eyes. The belly lacks pigment. Pigment is most discrete in juveniles. The caudal base is light, but darkens distally to a nearly black distal margin; all other fins are nearly devoid of pigment.

Lappets are absent. Prickles are usually present on dorsal and ventral surfaces from about the level of the anterior margin of eye to the posterior end of the dorsal base, often extending well onto caudal peduncle; prickles are often only sparsely distributed on the cheek. Dermal scale-like structures are present over most of the body (see description of *Sphoeroides*).

Colomesus psittacus is a large, heavy-bodied species; the largest specimen examined was approximately 325 mm (about 13 inches) total length.

Ecology and Distribution: *Colomesus psittacus* inhabits brackish and marine waters along northern South American coasts. Durand (1961:43) reported this species as the most common teraodontid to depths of 5 m off the Guianan coasts. Price (1955:27) reported that the species occasionally enters fresh water in Trinidad.

Collections indicate that this species extends from the Gulf of Paria, Venezuela eastward and southward along the South American coast to Aracaju (south of Recife), Brazil (Fig. 28). Tyler (1964:141) predicted its range at least eastward to the Amazon, although he had no specimens east of French Guiana. I have located a series (BMNH; 13, 11-52) from

Marajo Island, Brazil at the mouth of the Amazon. A specimen in the same series is *C. asellus,* indicating sympatry of the two species. A single specimen from Aracaju, Sergipe, Brazil (MZUSP 7665) is definitely *Colomesus psittacus.* Although this would approximately double the known range, I find no reason to question the data, as specimens of other species were collected by the same individual, N. A. Menezes, on the same date, July 1961, and from the same locality.

Colomesus asellus (Müller and Troschel) Amazon Puffer
(Figs. 25 and 27)

Chelichthyes asellus Müller and Troschel 1848b:641 (original description, Barima River, northwest British Guiana).

Chelichthyes psittacus Steindachner, 1861:141 (description, figure, Rio Branco, Brazil and unspecified localities in West Indies, in part).

Tetrodon psittacus. Günther 1870:286 (fresh waters of Guyanas and Brazil, in part). Cope 1878:298 (Brazil). Boulenger 1897:298 (Ilha do Marago, Brazil, in part). Goeldi 1898:461 (Rio Moju, at mouth of Rio Tocantins near Belem do Para, and "Ilha das Oncas," location ?). Puyo 1949:248 (description, figure, French Guiana, in part).

Colomesus psittacus. Jordan and Edwards 1886:244 (synonymy, Guiana, Brazil, in part). Eigenmann and Eigenmann 1892:73 (South America, in part). Gill 1892:714 (fig. of skull, in part). Jordan and Evermann 1898:1740 (South America, in part). Eigenmann 1905: 484 (South America, in part). Eigenmann 1912:529 (British Guiana). Fowler 1914:579 (Brazil). Ribeiro 1915:page 17 of Tetraodontidae section and 1918:68 (Brazil, in part), and 1920:4 (tributary of Rio Madeira, Est. Amazonas, Brazil). Jordan, Evermann, and Clark 1930: 500 (check list, in part). Fowler 1931:410 (Venezuela), and 1940a: 289 (Brazil). Eigenmann and Allen 1942:409 (synonymy, distribution, Peruvian headwaters of Amazon). Fraser-Brunner 1943:12 (osteology, in part). Colman and Cooper 1954:133 (Barima River, British Guiana). Santos 1954:159 (Brazil, in part). Le Danois 1959: 212 (systematics, in part). Pinto 1959:5 (osteology, Brazil). Ribeiro 1961:4 (Brazil).

Colomesus asellus. Tyler 1964:119 (systematics).

Discussion of Synonymy: *Colomesus asellus* was described as *Chelichthys asellus* by Müller and Troschel (1848b:641) from the Barima (originally Barama) River of British Guiana. As established by Tyler (1964:127), the first species associated with *Chelichthys* was *pachygaster,* a species not congeneric with those of *Colomesus,* but an atypical form of *Sphoeroides* (see earlier discussion under synonymy of *Sphoeroides* and Tyler 1964:122-128 for more detailed background). Despite the diagnostic characters included in the original description of this species, Günther (1870:286) followed an error of Steindachner (1861:141) and considered

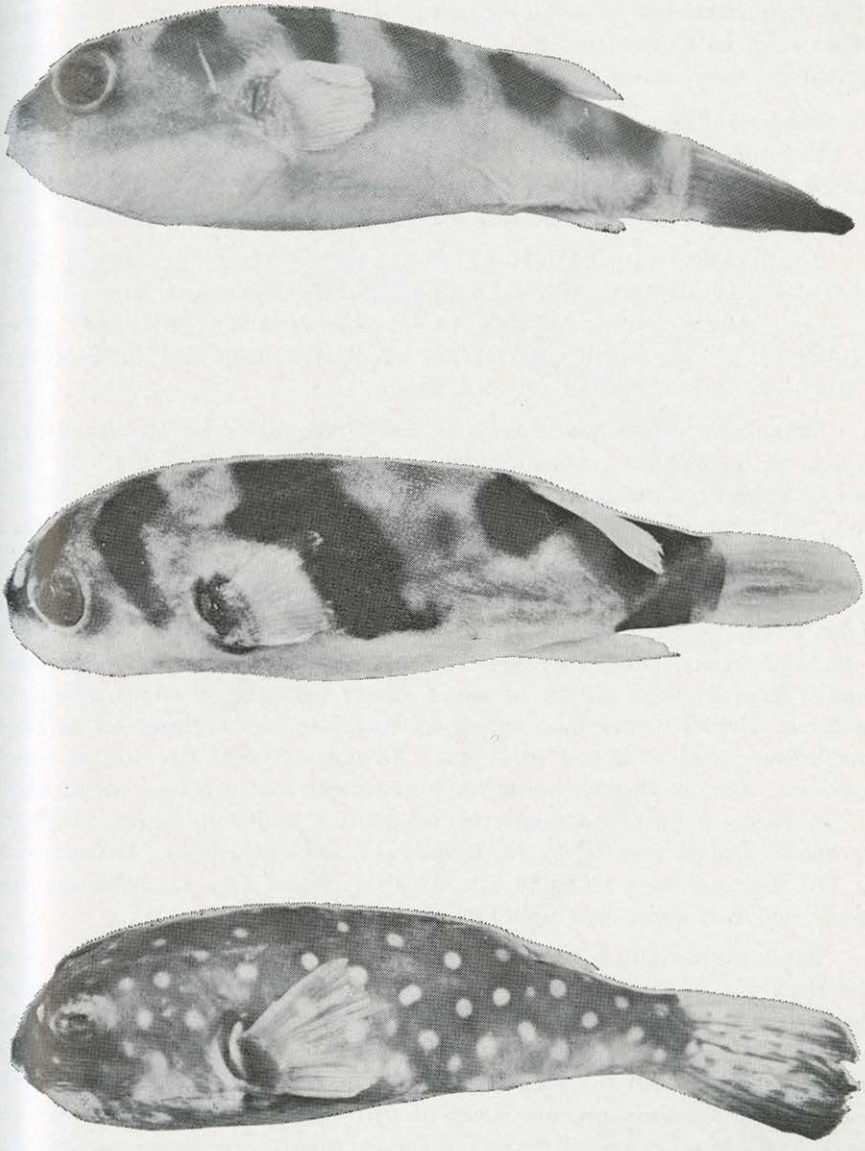

Figure 27. Upper: *Colomesus psittacus* RMNH 21534 (60 mm SL), Surinam. Middle: *Colomesus asellus* FSU 17521 (58 mm SL), Peru. Lower: *Ephippion guttifer* RGMC 127754 (106 mm SL), Republic of the Congo.

these two forms to be color variants of the same species. Subsequent works referred to this species as *psittacus,* until Tyler (1964:119) demonstrated the distinctness of the two forms.

Material Examined: Tyler (1964:43) examined 85 specimens, 19.6 to 128.4 mm SL from rivers and pools of Peru, Brazil, Venezuela, and British Guiana. In addition, I have examined 11 series of 17 specimens listed below; tables and descriptions are drawn from both sources.

South America: BMNH (2, 63-85), River Mazaruni, USNM 66167 (1, 59) British Guiana. BMNH (1, 64), Mouth of Amazon River, BMNH (1, 71), Marajo Island, MZUSP (2, 35-37), 7666 (1, 30), and USNM 191569 (3, 37-62), Brazil. FSU 17521 (2, 22-58), USNM 175994 (1, 36), 176112 (2, 33-44), 176113 (1, 50), Peru.

Diagnosis: *Colomesus asellus* is easily recognized by the large black blotch on the ventral surface of the caudal peduncle (Fig. 26). In addition, it has 5 broad transdorsal bars, 10-12 dorsal rays, and 13 to 16 pectoral rays. A transverse row of small indiscrete lappets borders the ventral margin of the chin.

General Description (Tables 2-4, 10): Head 2.4 to 2.8 in SL. Snout short, about 2.6 in head, shorter in juveniles. Eye moderately small, 4 to 7 in head. Least bony interorbit flat to very slightly convex, very broad, usually broader than length of snout, about 0.8 to 1 in snout, about 2.5 in head. Dorsal longer than snout, 0.6 to 0.8 in snout, about 1.8 in head; anal about equal to dorsal in length. Dorsal and anal fin origins nearly opposite. Caudal slightly rounded, long, about 0.6 to 0.7 in snout, about 1.7 in head. Pectoral moderate in length, 0.8 to 0.9 in snout, about 2.2 in head. Dorsal rays 10 to 12, usually 11, anal rays 8 to 11, usually 10 or 11. Pectoral rays 14 to 16 (rarely 13); caudal rays 11, with the first upper and two lower rays unbranched.

Basal pigmentation of upper surfaces is light brown or gray, with five dark, prominent transverse bars. The first extends between the orbits, the second and third across the middle of back, the fourth across dorsal fin base, and the fifth across caudal peduncle. The third bar is broader than the others, and the light interspaces nearly equal the width of the bars. A darkened area, reminiscent of still another bar, is present on the snout (Fig. 26). A small, slightly darkened area is sometimes present posterolateral to the eyes. The belly is unpigmented except for an area of very rich, dark pigmentation on the ventral area of the caudal peduncle (Fig. 26). This is frequently joined to the most posterior transdorsal bar by a shaded area on the lateral part of the caudal peduncle. All fins are mostly unpigmented except the distal portions of the caudal which may be dark in large specimens.

Lappets are present around the mouth, on the snout and chin; they are especially evident on the chin of large specimens, but may be inconspicuous in juveniles. They tend to follow the course of the lateral line

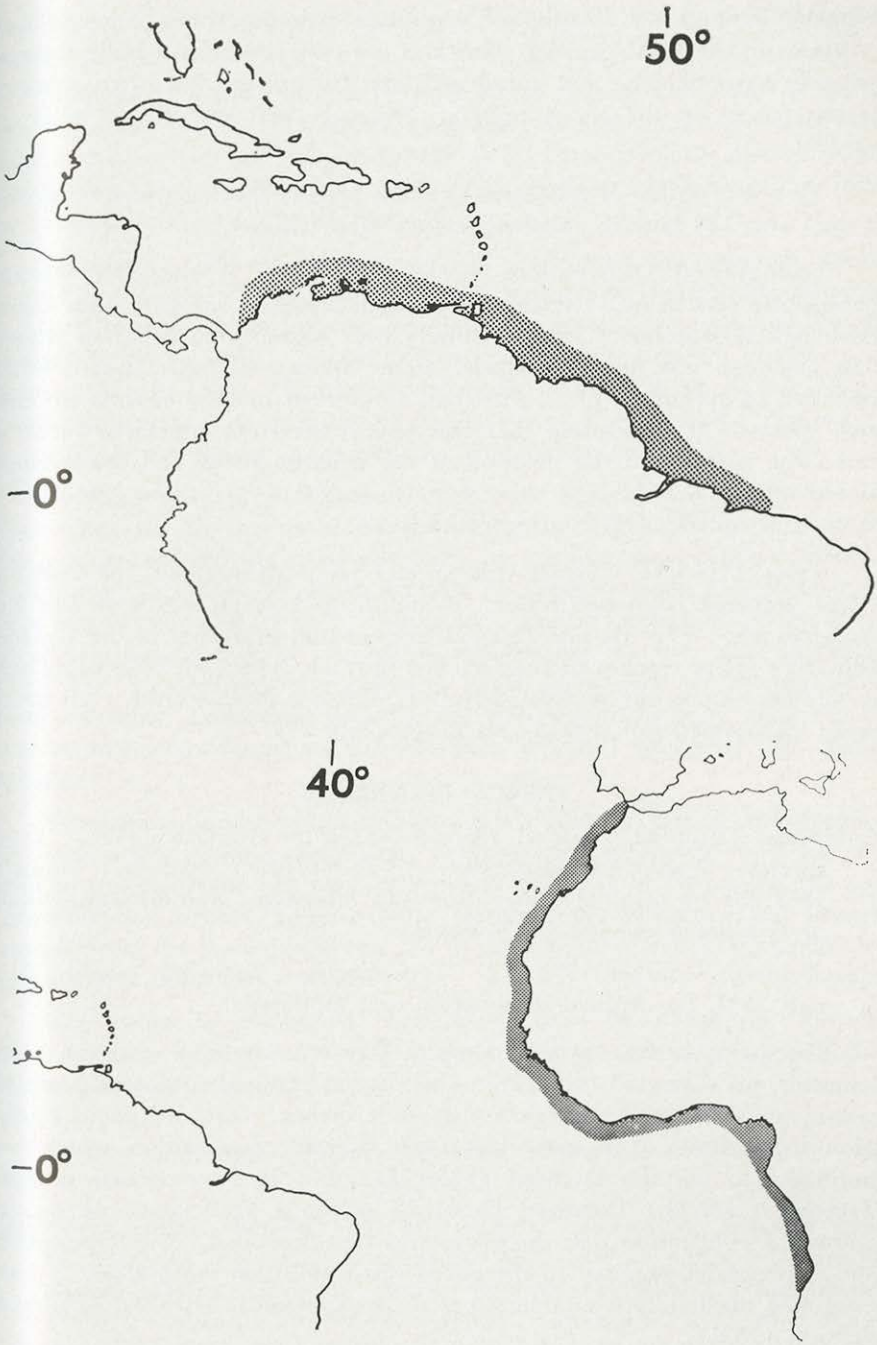

Figure 28. Upper: Distribution of *Colomesus psittacus*. Lower: Distribution of *Ephippion guttifer*.

branches around the mouth and the anterior snout, but do not extend posterior to the nasal papillae. Prickles are present on most body surfaces between nasal papillae and dorsal and anal fin origins, but often weak or inconspicuous in the cheek region. No scale-like dermal structures are evident.

This is a puffer of moderate size, the largest specimen examined (by Tyler) was 128 mm SL (about 6 inches total length).

Ecology and Distribution: *Colomesus asellus* is the only western hemisphere species of Tetraodontidae which normally inhabits fresh water. Although no specimens have definitely been taken from brackish waters, one specimen was among material from "Marajo Island", Brazil which included 13 specimens of *C. psittacus,* considered to be a marine or estuarine species. It is possible that this series was from brackish water, as this large island is at the junction of the Amazon River and the Atlantic Ocean. Tyler (1964:143) was able to maintain *C. asellus* for several months in aquaria with 10 o/oo rocksalt.

Tyler (1964:141) listed this species from throughout the Amazon River drainage from headwaters to mouth, and as far south as the Rio Araguaia (15° S.). He also listed it from coastal drainages of the Guianas and from lower reaches of the Orinoco near its delta. He also postulated its presence along the middle and upper portions of this river. All specimens I examined fall within this range (Fig. 25).

GENUS *EPHIPPION*

Ephippion (Bibron) Troschel 1856, p. 88 (after Duméril 1855). Type-species: *Ephippion maculatum* (=*E. guttifer*) (Bibron) Duméril 1855:281 by original designation and monotypy, and by Latinization of *Ephippion guttifer* by Troschel.

Hemiconiatus Günther 1870:272. Type-species: *Tetrodon guttifer* Bennett 1831, by original designation and monotypy.

Discussion of Synonymy: Despite Bibron's excellent work on tetraodontids, his disregard for previous works has resulted in nearly complete synonymy of his many generic and specific names. Only his genus *Ephippion* still stands. The name was from Bibron's manuscript, which was published in part by Duméril (1855:281), but in a vernacular context. Troschel (1856:88) Latinized Duméril's names a year later. It was in Duméril's publication that the genus was first described. The type-species and only species assigned to the genus was *Ephippion maculatum.* I have examined the holotype and found it to be conspecific with *T. guttifer* of Bennett (1831).

Günther 1870:272 overlooked the work of Bibron, as well as Bleeker's (1865) critical review of Bibron's system, both of which contained diagnoses of *Ephippion.* He created the section *Hemiconiatus* of the genus *Tetro-*

don, and assigned *Tetraodon guttifer* of Bennett as the type (and only) species of *Hemiconiatus.*

Subsequent publications have referred to one or the other of these genera. Gill (1892:713) briefly reviewed the historical aspects of the generic name. He also judged *Ephippion* to be sufficiently distinct from *Ephippium,* used by Bolten in 1798 for a molluscan genus and in 1802 by Latreille for a genus of dipterous insect, to be valid.

Diagnosis: The lateral ethmoids of *Ephippion* are separted above mainly by the mesethmoids, with partial separation by the frontals, whereas in other Atlantic Tetraodontidae, the lateral ethmoids are separated almost entirely by the frontals. In addition the entire skull is much broader and heavier than in other Atlantic tetraodontids. About 20 (8 + 12) vertebrae are present. The osteology is similar to the closely related *Tetraodon,* but differs in a longer, more anteriorly placed mesethmoid.

Ephippion is easily distinguished from all other Atlantic genera of Tetraodontidae by the specialized nasal organs which, by absorption of the septum between the nasal openings, has resulted in a single confluent opening on each side, bordered laterally by elongate flaps, and posteriorly by a less evident flap (Fig. 1). In other Atlantic tetraodontids, the nasal organ is a simple tube or tubular papilla bearing the two nasal openings (Fig. 1). In addition, subadult and adult *Ephippion* are distinguished from all other Tetraodontoidei by the presence of a bony carapace or corselet of armor formed by the expanded roots of the dorsal and lateral prickles.

The lateral line system of *Ephippion* is similar to that in *Sphoeroides,* but with a few notable exceptions: the posterior dorsal arm does not extend to the peduncle, but turns ventrad at the level of the dorsal fin and intersects the distinct posteroventral element; the posteroventral branch extends from the level of the anal fin to the middle of caudal peduncle; no anterolateral branch is present.

The genus is monotypic, represented only by *Ephippion guttifer* from Atlantic waters of the African coast. Other characters are included in the description of that species.

Ephippion guttifer (Bennett) Corselet Puffer
(Figs. 27 and 28)

Tetrodon guttifer Bennett 1831:48 (original description, Atlantic coast of northern Africa). Rochebrune 1882:178 (Gambia, Casamence, Faleme, Dakar, Goree). Osorio 1890:59 (Benguela). Ehrenbaum 1915:78 (description, West Africa). Metzelaar 1919:297 (Cape Blanco). Chabanaud and Monod 1926:287 (Cape Blanco). Monod 1927:739 (Cameroun). Daget and Iltis 1965:56 (Ivory Coast, considers *Tetrodon pustulatus* Murray a junior synonym—see discussion of synonymy below).

Ephippion maculatum (Bibron) Duméril 1855:281 (original description, only species of *Ephippion* listed, used in vernacular sense).

Ephippion maculatum (Bibron) Troschel 1856:88 (after Duméril).

Tetrodon (*Hemiconiatus*) *guttifer.* Günther 1870:272 (original description, Gambia). Steindachner 1894:90 (description, Liberia).

Ephippion guttifer. Gill 1892:713 (historical review of the genus). Buen 1926:57 (mar de Alboran). Fraser-Brunner 1943:13 (osteology). Irvine 1947:217 (description, Gold Coast). Rey 1952:351 (Gibralter to Angola, Mediterranean). Poll 1959:336 (description, Angola, considers *Tetrodon pustulatus* Murray a junior synonym).

Tetraodon (*Ephippion*) *guttifer.* Y. Le Danois 1959:166 (systematics) and 1961:468 (considers holotype of *Ephippion maculatum* of Bibron to be *Tetraodon* (*Ephippion*) *guttifer*).

? *Tetrodon pustulatus* (not of Murray). Pellegrin 1914:87 (Gabon). Fowler 1919a:267 (Gabun, French Congo) and 1936:1113 (Gaboon).

Hemiconiatus guttifer. Fowler 1936:1104 (synonymy, description, figure, mouth of Congo River). Cadenat 1950:285 (Senegal).

Discussion of Synonymy: The distinctive diagnostic characters of *Ephippion guttifer* have resulted in little taxonomic confusion regarding this species. Only two specific names (*maculatum, pustulatus*) other than the correct specific designation of *guttifer* have been assigned to this form.

Bennett first described the species as *Tetrodon guttifer* in 1831 (p. 148). His description was diagnostic (white spots on olive brown, D. 11, A. 10, P. 21) of an immature specimen, and Günther (1870:273) stated that although the holotype was apparently lost, there is no difficulty in identifying the species he had in mind. No other marine or estuarine form from the west coast of Africa (the type-locality) is at all similar to *Ephippion guttifer* in pigmentation or fin ray counts.

The manuscript of Bibron designated the type and only species of *Ephippion* as *maculatum.* This manuscript name was first published by Duméril 1855:281 (in vernacular context) with a generic diagnosis based on the species *maculatum.* Troschel (1856:88) Latinized the Duméril work. *Ephippion maculatum* (Bibron) Troschel is conspecific with the *Tetrodon guttifer* of Bennett.

On several occasions *Tetrodon pustulatus* has been included in the marine fauna of western Africa (Pellegrin 1914:87, Fowler 1919:267 and 1936:1113). While insufficient description was included in these works to determine specific identification, it is probable from the collection localities that the specimens were immature *Ephippion guttifer* which had not yet developed the distinctive carapace. Poll (1959:339) and Daget and Iltis (1965:56) have proposed that *T. pustulatus* (a species described from "Old Calabar", Africa, 1857) is a junior synonym of *Ephippion gutti-*

fer and was described from a juvenile. However, I have examined the types of *Tetrodon pustulatus* and find them to be distinct from *Ephippion guttifer*. The largest unmutilated type-specimen of *T. pustulatus* is 248 mm SL and lacks any indication of a carapace. This is much larger than the size of specimens of *Ephippion* with a well developed carapace. Other differences include caudal shape, certain proportions, pigmentation, and pattern of prickle development (absent on head of *E. guttifer*, present on head of *T. pustulatus*). In addition, Boulenger (1907:543) listed *T. pustulatus* as an African freshwater species.

Material Examined: Eighteen series, 26 specimens.

Types: MNHN 2155 (1, 402), Goree, *Ephippion maculatum* (Bibron) Troschel "Genotype de *Ephippion*" of Bibron. **Africa:** ANSP 103236 (2, 112-136), Liberia. BMNH (1, 113), BMNH (1, 77), Accra, Ghana. UMML 21609 (1, 59), ANSP 109738 (1, 374), Nigeria. BMNH (1, 121), Eloby district, Gabon. RMNH 291 (1, 107), Gabon. RMNH 7543-7545 (3, 32-107), 7686 (1, 169), 127753-127754 (2, 91-106), 128312-128314 (3, 121-174), 56184-56186 (3, 22-49), 56203-56205 (3, 23-37), 56292 (1, 130), Republic of the Congo. RMNH 80179-80180 (2, 133-141), 127750 (1, 380), Angola. BMNH (1, 114), Five Cowtie Creek, not located to country.

Diagnosis: *Ephippion guttifer* is easily distinguished from all other Atlantic puffers by its trilobed nasal organ (Fig. 2) which surrounds a single, exposed nasal opening and the presence of a rigid carapace in subadults and adults. The caudal fin bears indistinct light spots similar to those on the body.

General Description (Tables 2-4, 11): Head about 3.1 in SL, slightly longer in subadults. Snout moderately short, 1.9 to 2.3 in head, longest in large adults. Eye moderate, usually 4 to 5 in head in subadults, although relatively smaller (6 or more in head) in large adults. Least bony interorbit flat, broad, 0.8 to 1.0 in snout length, about 2.2 in head. Dorsal relatively long, about 0.7 to 0.8 in snout, about 1.5 in head; anal slightly shorter, about 0.7 to 0.9 in snout, about 1.6 in head. Dorsal fin origin over anus, slightly anterior to anal fin origin. Caudal emarginate in juveniles and subadults, but lunate in older specimens. Caudal long, about twice snout in subadults, but relatively shorter (about 0.8 in snout) in large adults, and 1.5 in head of large adults. Pectorals of moderate length, usually 0.9 to 1.2 in snout, about 2.1 in head. Dorsal rays 9 to 11, usually 10, anal rays 8 to 10, usually 9. Pectoral rays 18 to 20, usually 19, with an uppermost pectoral rudiment, not included in the ray count. This rudiment is particularly well developed in this species, often about half the length of the first complete ray. Caudal rays 11, with the first upper and one or two lowermost rays unbranched.

Basal pigmentation of upper surfaces is a rich brown, sometimes with a slight maroon tinge. This pigmentation fades laterally and disappears,

resulting in an unpigmented belly. The pigmented surface is covered with discrete white spots, about a third to a fourth the eye diameter. These are always evident laterally, but may be less conspicuous or absent on the dorsum. The caudal is pigmented similarly to the lateral body surface, but the caudal rays tend to disrupt the distinctness of the spots; other fins may be slightly dusky, but are mostly unpigmented.

Lappets are absent. Ventrally, prickles are present to near the anus; the head is naked. On the dorsal and lateral surfaces of the trunk, prickles are present and much modified with enlarged, bony bases that form a carapace of scute-like plates. There are no sharp, exposable projections from these plates. The carapace encloses the dorsum and flanks from about the level of the pectoral fin base to dorsal and anal fin origins. Fine integumentary striations which resemble orifices of vestigial or undeveloped scutes extend posteriorly to the peduncle. According to Poll (1959: 338), carapace development is not evident until individuals attain 225 mm SL. In very large individuals (350 mm or more), the carapace is an extremely rigid, bony structure, reminiscent of similar structures in cowfishes and trunkfishes (Ostraciontidae).

Ephippion guttifer is a very large puffer, which attains 800 mm (almost 3 feet) total length (Daget and Iltis 1965:56; Le Danois 1959: 168).

Ecology and Distribution: Study material indicates that *Ephippion guttifer* is a marine and estuarine species. Fowler (1936:1106) noted specimens from the mouth of the Congo River, and Daget and Iltis (1956:56) listed it from "Baie De Cocody" and "Lagune Eber" of the Ivory Coast. The Guinean Trawling Survey collected this species from many offshore localities. Poll (1959:336) also cited offshore collections of this species. Among material examined, a collection from water 24 meters deep off the coast of Nigeria was the maximum depth recorded for this species.

Rey (1952:351) reported *Ephippion guttifer* from Gibraltar, and Malaga, Spain in the Mediterranean, and Buen (1926:57) listed it from the Mar De Alboran in the extreme southwestern Mediterranean off the coast of Morocco. The species apparently extends from near these locations along the entire Atlantic coast of Africa to Angola, near Benguela, from where Osorio (1890:59) reported it (Fig. 28).

PHYLOGENY OF ATLANTIC GENERA AND SPECIES OF TETRAODONTIDAE

The four genera of Atlantic Tetraodontidae probably do not represent generic divergence from a common ancestral stock within that ocean. Rather, they appear to have stemmed from at least two distinctive groups, some of whose geographic origins may never be determined with any degree of certainty. Three of the genera, *Lagocephalus, Sphoeroides,* and *Colomesus* appear closely allied, and may well demonstrate radiation within

the Atlantic Ocean. *Ephippion,* however, appears more closely allied to a number of Indo-Pacific forms.

It would be futile to speculate on precise intergeneric relationships of Atlantic genera without a knowledge of the entire suborder Tetraodontoidei on a world-wide scale. Such would require an undertaking of many years study, and far more study material than is presently available. The most diverse assemblage of teraodontids is that of the Indo-Pacific region, which unfortunately, as Tyler (1964:126) stated is ". . . the group of Plectognath fishes which are perhaps the most poorly known." Perhaps this region is the center of origin for the tetraodontids.

Previous work on the hierarchal systematics of the group has been sketchy and incomplete, due primarily to lack of study material. Fraser-Brunner (1943) provided the most recent attempt to define intergeneric relationships within the Tetraodontoidei, but his 18-page account is far from complete. I have chosen to ignore the work of Le Danois (1959), the fallacies of which were discussed earlier (p. 12). All ichthyologists concerned with higher systematics in general, and plectognaths in particular, await the completion of the study by James C. Tyler on the hierarchal systematics of the plectognath fishes which will undoubtedly provide the most complete osteological account of the order to date.

For these reasons, I present only those inferences which can be logically drawn at present regarding the phylogeny of Atlantic genera. However, I shall attempt to relate a much more detailed account of intrageneric phylogeny of *Sphoeroides,* the dominant genus of tetraodontids within Atlantic waters. A discussion of principles employed to determine these relationships is included in the section devoted to that genus.

LAGOCEPHALUS

Previous workers (Regan 1902:292; Fraser-Brunner 1943:4) have considered *Lagocephalus* to be one of the more primitive tetraodontoid genera. In fact, Fraser-Brunner considered it as the most primitive genus from which even the aberrant Canthigasteridae (sharp-nosed puffers) and Molidae (ocean sunfishes) were derived.

Modern concepts of phylogeny generally prevent consideration of an extant group to have been the direct progenitor of another such group (Mayr 1969:214). In many respects *Lagocephalus* represents a highly specialized genus, especially by its adaptations to a pelagic habitat (i.e. lunate caudal; long, falcate dorsal, anal, and pectoral fins; countershading with silver flanks typical of pelagic fishes; and streamlined elongate general body shape; Figs. 2, 3, and 5). At least one pelagic species, *L. lagocephalus,* is circumglobal. Such a habitat seems an unlikely origin for a group such as the puffers whose adaptations are so specialized for grazing and browsing on hard-bodied benthic organisms. However, a number of morphological characters of *Lagocephalus* may be relatively generalized,

and this genus may in fact be close to the early tetraodontoids. The more pertinent of these are discussed below.

The nasal organ of *Lagocephalus* consists of a short low papilla with two nasal openings (Fig. 1). This condition is considered ancestral (Regan 1902:292), and is also found in balistids and diodontids, as well as in several genera of tetraodontoids. Nasal organs have become highly modified in various plectognath genera (see discussion of nasal organs under *Ephippion* below).

The prickles of *Lagocephalus* appear to be unspecialized and similar in structure to those of many other tetraodontoids. Although it is difficult to assess the generalized condition of these structures, *Lagocephalus* obviously does not share a derived condition of prickle specialization such as is found in *Ephippion, Diodon,* or some other genera of plectognaths.

Study of the cranial osteology of *Lagocephalus* reveals a similarity between it and the much specialized ocean sunfishes (Molidae). Fraser-Brunner (1943:4) stated that apart from the fusion of the jaws into a single upper and lower element "the skull (of molids) is almost exactly similar to that of *Lagocephalus,* even possessing the posterolateral limbs of the frontals characteristic of that genus." This similarity indicates cranial affinities to the ancestral condition, but conclusions as to its significance should await further study of the higher systematics of the order.

Cranial and external morphological characters of *Lagocephalus* doubtlessly reveal close relationships between it and *Sphoeroides,* both of which are probably best considered in a subfamily together with the Indo-Pacific genera *Amblyrhynchotes, Torquigener,* and the South American *Colomesus.* However, it is difficult to assess generalized and specialized characters within this group. All are obviously highly specialized for their particular habitats.

Among Atlantic members of the genus, *Lagocephalus lagocephalus* is circumglobal, and *L. laevigatus* is trans-Atlantic. However, *L. lagocephalus* is certainly the more pelagic of the two species, and is more highly modified for a pelagic habitat (see discussion under species accounts). If it is assumed that the genus arose from a less pelagic ancestral stock as stated above, then it is logical to consider *L. lagocephalus* as the product of extreme specialization, while *L. laevigatus* may be closer to the ancestral generic origin. Relationships to other members of the genus are unknown; no other species of *Lagocephalus* are of world-wide distribution, perhaps reflecting less pelagic specialization of these other forms.

SPHOEROIDES

The genus *Sphoeroides* appears to be an extremely close ally to both *Lagocephalus* and *Colomesus.* The structure of the nasal organs is essentially identical to that found in the other two genera, and is nearly constant within the entire genus (Fig. 1). The cranial osteology of *Sphoeroides*

reveals extremely narrow, fragile bones, but their relative positions are as in *Lagocephalus.* In both *Lagocephalus* and *Sphoeroides* the mesethmoid is very elongate, resulting in a prominent snout; however, in *Lagocephalus* the mesethmoid is broad and heavy, while in *Sphoroides* it is extremely thin and light. The frontals are much more elongate and narrow in *Sphoeroides,* but they lack the elongate posterolateral extensions of *Lagocephalus.* In both these genera and in *Colomesus,* the anterior frontal processes separate the lateral ethmoids which are separated principally by the mesethmoids in *Tetraodon* and related genera (see under *Ephippion* below). *Sphoeroides* has a much reduced dorsal and anal fin ray count (8 and 7) compared to *Lagocephalus* (13-15 and 11-13); *Colomesus* is intermediate (9 to 12 for both fins; Tables 3 and 4). Most authors consider the lower number in *Sphoeroides* as a specialization.

Intrageneric Relationships of *Sphoeroides*

Consideration of phylogeny within *Sphoeroides* requires a careful assessment of various characters used as criteria. The terms "primitive", "advanced", "generalized", and "specialized" are relative terms whose frame of reference must be clearly delineated, in this case within the genus *Sphoeroides.* It is not my intent to enter into a philosophical discourse on the usage of these terms. Such can be found in almost any recent text on phylogeny or evolution (e.g. Eaton 1970:208; Mayr 1969:213; Henning 1966). However, it must be remembered that because species or populations share one or several generalized or ancestral characters does not necessarily indicate closeness of kinship. Conversely, sharing of specialized or derived homologous characters does indeed indicate a close relationship (Mayr 1969:202, 214, 220; Henning 1966).

A number of traits used in the determination of the phylogeny of the species of *Sphoeroides* will be discussed. With each is included reasons for that character's consideration as "ancestral" or "derived". Utilization of these self-explanatory terms rather than the more ambiguous "generalized-specialized", or "primitive-advanced" follows recommendations by Mayr 1969:213).

Pigmentation patterns of variably pigmented groups such as puffers, blennies, gobies, certain reef fishes, and other fishes are especially useful because patterns are so variable through time that close resemblances of patterns can logically be considered as sharing a derived character, while the ancestral patterns can rarely be known and usually would not be possessed by any extant species of a group. This can be considered a character of extremely "high weight", that is, one which can be confidently cited as revealing phylogeny (Mayr 1969:220). Two basic categories of pigmentation patterns, caudal and trunk, are useful in *Sphoeroides.*

The caudal pattern of pigmentation is either of a dusky dark caudal fin with light, unpigmented distal tips (*Sphoeroides pachygaster* alone

possesses this pattern) or of a barred condition with proximal and disal dark bars separated by a central light bar (Fig. 2). The discreteness of this latter condition varies from barely noticeable to extremely distinctive. Although possession of a common degree of discreteness may indicate relationships, such can be used only with great care as corroborative evidence in conjunction with other characters. It could be justifiably argued that parallel patterns of caudal pigmentation distinctness could arise rapidly, a result of local ecological conditions (i.e. in clearer waters, more distinct patterns might be expected). The simplicity of the caudal pattern (thus the possibility of its origin by convergent evlution) makes this patterns a less reliable phylogenetic indicator than trunk pigmentation.

The pigmentation of the trunk is an extremely complex and variable character in this genus. Four major patterns of pigmentation are found among Atlantic species. One pattern consists of solid pigmentation, occasionally with a few lateral spots, such as is found in *S. pachygaster* (see Fig. 13). Another pattern consists of discrete round spots against a light lateral streak along the flanks, with large irregular blotches of nearly solid pigmentation on the dorsum. This pattern with some minor variations is found in *S. marmoratus* and *S. spengleri,* as well as in one or more eastern Pacific species (*S. angusticeps* and *S. lobatus* as presently understood). A third and similar pattern has less uniform lateral spots which may be modified into blotches or bars, and a dorsum which is more spotted or blotched and ornamentad with light green or white vermiculations (*S. tyleri, S. nephelus, S. parvus,* and *S. maculatus*). The final pattern consists of a dorsum of light, coarse arches and circular markings against a dark background (Fig. 10), often with many small lateral spots. Such is found in *S. testudineus* in the Atlantic as well as in *S. annulatus* and its close relatives in the eastern Pacific. *Sphoeroides greeleyi* also shows a distinctive indication of such a pattern (Fig. 10), although dorsally the pattern is interrupted by spots and blotches and in some ways appears similar to the third pattern. More or less aberrant patterns are found in *S. dorsalis, S. yergeri,* and *S. georgemilleri.*

Lappets can be categorized into two groups. The first is the small black dorsal pair in the middle of the back (see Fig. 8). These are apparently derived, as they are found in the morphologically similar *S. marmoratus, S. angusticeps, S. lobatus,* and *S. dorsalis.* The second category includes lappets which are tan or nearly white (see Fig. 8), and scattered on the flanks. These are apparently a more ancestral character as they are possessed by such diverse species as *S. marmoratus, S. spengleri, S. yergeri, S. tyleri, S. greeleyi,* and the Pacific species *S. lobatus,* while they are lacking in other species closely allied to these forms. Lappets are present around the jaws of *Colomesus asellus,* but it is unclear whether these are homologous structures.

Prickles are certainly an ancestral character, as they are possessed by

all tetraodontoid and diodontoid genera. In *Sphoeroides* their loss could only be considered as the derived condition, but this may occur independently. *Sphoeroides nephelus* occasionally lacks prickles and *S. pachygaster* always lacks prickles, but the two are obviously unrelated. There does not appear to be any unusual modification of prickles which could be considered as a specialized condition in this genus.

Scale-like dermal structures are present along the flanks of a number of relatively closely related (by previous criteria) species, and thus would appear to be a derived character. However, the condition is also present in *Colomesus psittacus*. While it probably arose independently, this trait must be used primarily in a corroborative manner. In *Sphoeroides* it is present in *S. greeleyi, S. tyleri, S. parvus, S. nephelus, S. maculatus,* and *S. georgemilleri.*

Fin ray counts are generally of no help in determining phylogeny at the species level in pufferfishes. It is impossible to determine the advanced condition except in extreme situations, and even then the possibility of parallel development may nullify the reliability of the character. In addition, it must be determined whether or not differences in the number of rays are caused by genetic or environmental factors.

Osteology is similar among the species in the genus *Sphoeroides.* Minor variations of relative lengths and widths of certain cranial bones, and resulting proportional differences exist, but these are of use mainly in a taxonomic sense. Only in *S. pachygaster* do significant differences reveal a trend. This species appears to be somewhat intermediate in position between *Lagocephalus* and *Sphoeroides,* with definite affinities to the latter. Unfortunately, adequate study material of this rarely collected deep water form is unavailable, and these conclusions are tenuous.

General body size is partially useful in isolating individual species which may have differentiated from a more generalized stock. A modest size of about 100 to 150 mm for adults seems to be the most common size within the genus. A few species in specialized habitats appear to have evolved larger sizes (e.g., *S. maculatus,* a temperate species).

Similarity of general body shape and contour, inherently revealed in proportional measurements, is occasionally used as a composite character in assessing phylogeny. Reference to the figures should be made for fuller appreciation of this character.

Finally, distribution and habitat may aid in reconstruction of the phylogenetic patterns of the group. For example, because nearly all tetraodontoids are tropical or subtropical, a temperate species would be expected to be quite specialized. These factors are discussed when applicable with each species or species group involved. Various other specialized or derived characteristics applicable to certain forms are discussed under individual species accounts.

A phylogram (Fig. 29) demonstrates postulated relationships within

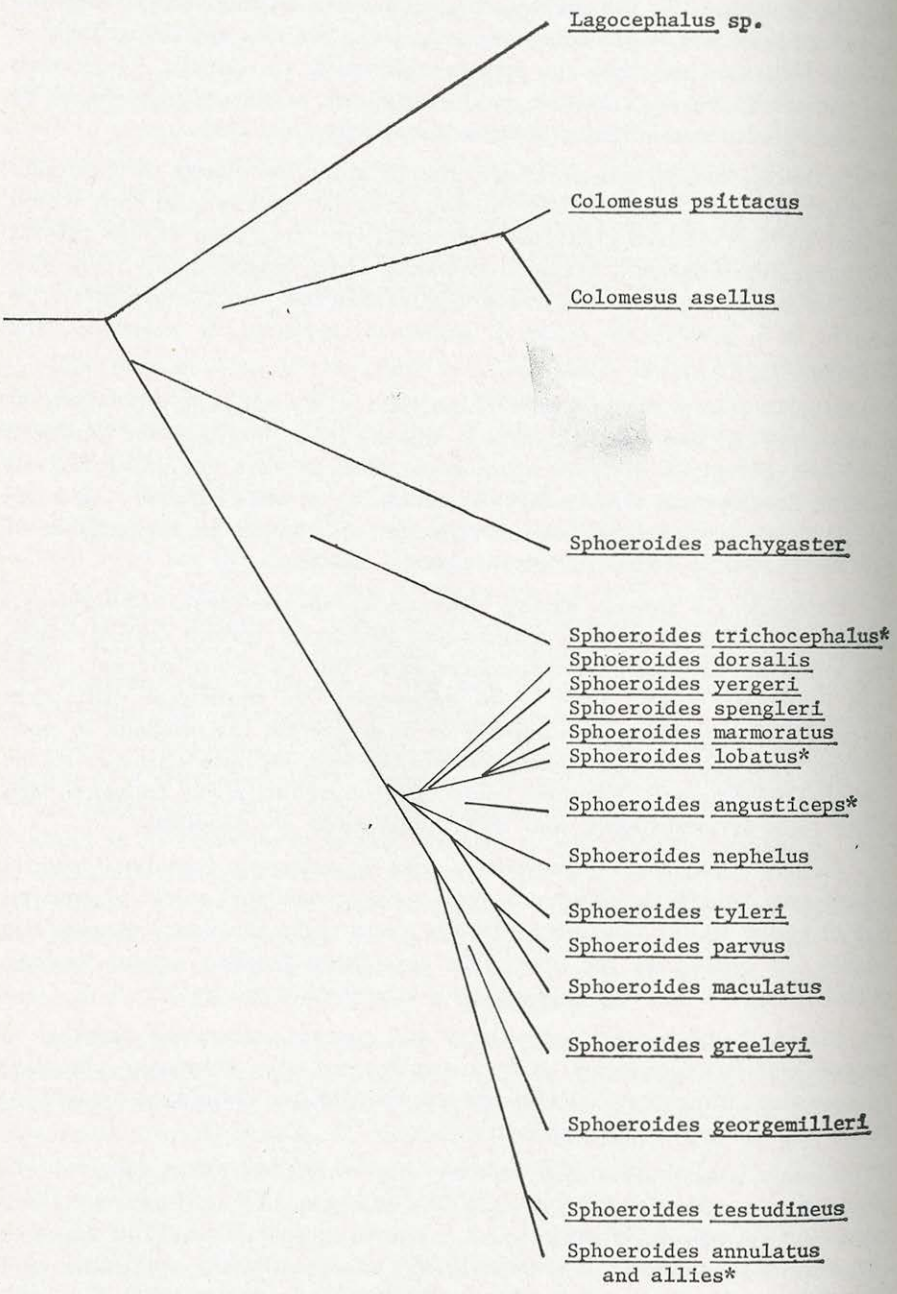

Figure 29. Phylogram of *Lagocephalus* and the species of *Colomesus* and *Sphoeroides*. *Pacific species.

the genus. It should be emphasized that this figure is diagrammatic in nature, provided as a visual aid to emphasize sequential relationships, and is not necessarily precise regarding degrees of specialization which may have occurred, nor the relative time involved.

Eastern Pacific species of *Sphoeroides* have been studied in a cursory fashion and have been tentatively included for completeness of treatment. However, extensive reevaluation of the systematics of these species is needed, and they are currently under study by Dr. Boyd W. Walker of the University of California at Los Angeles. These species are designated by an asterisk in the phylogram.

Sphoeroides pachygaster is doubtlessly the most divergent and "atypical" species of *Sphoeroides.* Although Fraser-Brunner (1943:11) stated that except for its lack of prickles this species (as *Liosaccus cutaneus*) "in other respects is obviously a *Sphaeroides*" it is aberrant from the other members of the genus. Its pigmentation pattern (uniform with an occasional area of spots on the back and sides) is unique in the genus. In addition, the caudal fin is dark with light distal corners, approaching the pattern of *Lagocephalus,* and quite distinctive from the barred pattern of other *Sphoeroides* (Fig. 2). The integument always lacks prickles and lappets. The osteology of *S. pachygaster* differs from other conspecific forms. The frontals are extremely broad, sometimes with cartilaginous lateral margins; the mesethmoid is relatively short and stout. This species is much more thick-bodied than any other *Sphoeroides.* The dorsal and anal counts (9 and 8) are atypical for the genus, usually 8 and 7 (Tables 3 and 4).

Apparently *S. pachygaster* diverged early from the ancestral *Sphoeroides* stock, which was close to the ancestral *Lagocephalus* stock. However, *S. pachygaster* certainly must be specialized for its deep water habitat which is atypical of the genus. Unlike other *Sphoeroides,* it has successfully established its range throughout most the world's tropical and temperate waters of moderate depth.

Sphoeroides trichocephalus is an eastern Pacific species evidently not closely related to any other *Sphoeroides.* More study of this form is required. Its taxonomic status (a junior synonym is *S. furthii*) has been treated by Shipp (1971:569).

Sphoeroides dorsalis, S. lobatus, S. angusticeps, S. marmoratus, S. spengleri, and *S. yergeri* are members of a relatively close-knit species complex. All share similar body proportions, and most are similarly pigmented.

Sphoeroides dorsalis is the most distinctive species of the complex, very likely a result of its preference for deeper water habitats. It possesses the pair of black dorsal lappets, a derived character present in most members of this group. Like other species in the complex, this form bears few prickles, often widely spaced, or absent in some areas on the body. However, it has secondarily lost the lateral lappets, and the typical pig-

mentation pattern of the complex has been greatly modified. The discrete lateral spots are lost or diffuse. In addition, *S. dorsalis* has developed sexual dichromatism unknown in all but one other species of the genus. The caudal fin usually shows well defined bars, typical of this species group, but the distal tips of the fin rays are often projected, apparently a species specific specialization (Fig. 2).

Sphoeroides yergeri appears less aberrant than *S. dorsalis,* but more so than the other more closely allied members of the complex. It has secondarily lost the black pair of dorsal lappets, but retains other lappets. The black lateral spots are lost and replaced by tiny black speckles, but the light background is quite discrete as are the caudal bars. In all other respects this form is similar to the remaining species of the complex.

Except for minor variations in pigmentation and morphology, the eastern Atlantic *S. marmoratus* and eastern Pacific *S. lobatus* are nearly identical. *Sphoeroides marmoratus* has a more sharply defined, easily recognized pigmentation pattern, although the basic pattern in both is the same. Both species have the dorsal black pair of lappets as well as lateral lappets. *Sphoeroides spengleri,* whose distribution in the western Atlantic separates the other two species is also nearly identical to both forms in pigmentation. However, *S. spengleri* has lost the black pair of dorsal lappets. These three forms have surely been recently isolated. *Sphoeroides lobatus* almost certainly diverged from the ancestral Atlantic stock after its isolation by the most recent emergence of Central America. *Sphoeroides marmoratus* and *S. spengleri* are tenuously isolated by the open Atlantic Ocean, but based on morphological criteria, this isolation has also been recent. These three species might prove to be conspecific if the geographic isolation were removed.

Sphoeroides angusticeps has not been examined by me, but based on all descriptions available, it is close to *S. dorsalis* or *S. lobatus.*

Sphoeroides nephelus, S. tyleri, S. parvus, and *S. maculatus* form another species complex. Based on general morphology, pigmentation, and common possession of scale-like dermal structures, the following hypothesis as to their phylogenetic history is presented.

Sphoeroides tyleri appears nearest to the ancestral stock in its possession of lappets, general body size, generalized body pigmentation (it lacks the specialized pigment characters discussed below), and its present distribution. This form occurs in one of the most speciose ichthyofaunal areas of the Atlantic, the southern Caribbean, which was probably the habitat of the ancestral population.

Sphoeroides nephelus is an extremely variable species which appears to have diverged relatively early from the ancestral mainland stock of this complex, and differentiated in the specialized environment of coral and clear water habitats of the Caribbean islands. Most noticeable in this respect are the highly colorful and variable pigmentation patterns (Fig. 23).

The lateral spots are distinct, and the sides and back are covered with distinctive light (greenish or bluish in life) vermiculations, reticulations, or circular markings. In some populations, mature, ripe males may become covered with small bright orange or red spots. Lappets are lost, as are prickles in some populations, and the snout has elongated (an adaptation to reef browsing?). *Sphoeroides nephelus* probably did not appear along the coast of mainland North America until it reached Florida after the emergence of the peninsula (Shipp and Yerger, 1969b:483).

Sphoeroides parvus and *S. maculatus* appear to have differentiated from an ancestral western North Atlantic stock. This western North Atlantic population was probably continuous along the southeastern coast of North America prior to the emergence of peninsular Florida. When this peninsula emerged, the Gulf of Mexico and temperate Atlantic populations were isolated. The closeness of these populations is attested by their common possession of a broad flat interorbit, extremely dense coverage of prickles, and essentially similar lateral pigmentation. In addition, *S. maculatus* has extensive coverage of tiny black spots (Fig. 9) found nowhere else in the genus except rarely on the cheeks of large adult *S. parvus*. Lappets are absent in both species. Some evidence of vague greenish (white in preservative) reticulations are found on the body of both species, but these are never as distinctive as in *S. nephelus*. *Sphoeroides parvus* has retained small size, and apparently in response to environmental factors of the muddy Gulf of Mexico, has developed a markedly diffuse pigmentation pattern. In contrast, *S. maculatus,* inhabiting the cool relatively clear waters of the western North Atlantic, has developed a large size, more pectoral fin rays, and discrete pigmentation, especially the lateral spots which have evolved into distinct lateral bars.

Absence of significant populations of any of these four species along Central American Caribbean shorelines may be a result of competitive exclusion by the extremely successful immigrant from the eastern Pacific, *S. testudineus*. Differentiation between present populations of *S. tyleri* and *S. parvus* may be due at least in part to their isolation by the intermediate population of *S. testudineus*.

Present zoogeographical patterns of the four species of this species complex support the above hypothesis, however the chronology of the events described above is unknown.

Sphoeroides greeleyi appears to be somewhat intermediate between the previous species group and the final species complex, *S. testudineus* and allies. Although *S. greeleyi* usually retains lateral lappets, and shares general body proportions and the dermal scale-like structures of the former species group, it definitely possesses the distinctive pigmentation pattern of the latter complex (Fig. 10). *Sphoeroides greeleyi* evidently is close to the progenitor stock which inhabited the shallow waters that covered and adjoined Central America before its emergence. The population isolated in the Caribbean by the emergence

of land gave rise to *S. greeleyi;* the population isolated in the eastern Pacific radiated into the many closely related forms here referred to as *S. annulatus* and allies.

The *Sphoeroides annulatus* complex is comprised of a group of closely allied forms, many of which are poorly known. All are characterized by relatively short snouts, broad interorbits, absence of lappets of either type, and a distinctive dorsal pattern of arch-like and circular geometric designs. The number of species of this group present in the eastern Pacific leaves no doubt as to their origin and radiation in this realm. However, one form, *S. testudineus,* has evidently evolved in the Caribbean from an *S. annulatus*-like immigrant which had reentered the Caribbean from the Pacific. It should be emphasized that *S. testudineus* is the most euryhaline member of the genus, and tolerates nearly fresh water (see ecology of *S. testudineus*). Therefore, an open seaway was not necessary for this species' progenitor to traverse the present land barrier of Central America; any continuous brackish waterway may have effectively eliminated the Central American land barrier. In any case, *S. testudineus* and *S. annulatus* are very closely related and it is possible that they are subspecies. The immigration to the Caribbean from the Pacific must have been quite recent.

On the basis of its abundance in the Caribbean, *S. testudineus* is a highly successful species. It is usually abundant wherever it is found. Persons who have collected specimens of this species for me have noted the large swarms that appear soon after bait is set out. This abundance is verified further by the large numbers of individuals in the series loaned from institutions.

It is possible that the success of *S. testudineus* was responsible for the isolation between the southern Caribbean and the western North Atlantic populations of the *S. tyleri-nephelus-parvus-maculatus* complex. Populations of this complex and of *S. testudienus* would have occupied similar inshore habitats, and competitive exclusion may have resulted in the extinction of geographically intermediate populations of that complex. *Sphoeroides testudineus* may also eventually out-compete or displace its close relative, *S. greeleyi.* Estuarine collections of *S. greeleyi* are usually accompanied by a far greater number of *S. testudineus.* Significant populations of *S. greeleyi* are from more open waters in a few isolated localities only, despite the large extent of the range of this species.

Sphoeroides georgemilleri appears to be an aberrant form which, perhaps in the deeper waters inhabited by the species, has lost much of the distinctive pigmentation that may have revealed phylogenetic affinities. On the basis of the vestiges of pigmentation, the presence of dermal scale-like structures and general body morphology, this form appears to be closest to *S. greeleyi.*

COLOMESUS

Colomesus is a distinctive genus with two species restricted to South

America, one freshwater and the other marine. Although its phylogenetic position is unclear, this form is certainly more closely related to *Lagocephalus* or *Sphoeroides* than to the *Tetraodon, Arothron, Ephippion* group. Although Fraser-Brunner (1943:12) considered the Colomesidae as a separate family, he stated that it was a "derivative from *Sphaeroides*-like stock".

The osteology of the genus is remarkable for the tremendous anterior extension of the sphenotics which in adults completely exclude the frontals from the margin of the skull. In other respects, the skull is basically similar to the *Lagocephalus-Sphoeroides* group, even to elongation of the mesethmoid. The nasal organs are also essentially the same as in other genera of this group (Fig. 1).

The two species of *Colomesus* are quite similar. On ecological grounds one might infer that the freshwater species *C. asellus* is more specialized. If one assumes the ancestral stock of tetraodontids to have been marine, as are all extant species of *Lagocephalus* and *Sphoeroides,* it would be logical to consider the basal stock of *Colomesus* to be marine also. In addition, *C. asellus* is probably a recent entrant into the fresh water fauna of South America, because it is the only freshwater tetraodontid in the Western Hemisphere. Had it been an ancient resident of the Amazon and its tributaries, adaptive radiation should have occurred.

EPHIPPION

Osteological features and structure of the nasal organ have been used most extensively in demonstrating relationships above the species level in the Tetraodontoidei. On these bases, several genera of African and Indo-Pacific puffers are evidently closely related. Fraser-Brunner (1943) included *Ephippion, Tetraodon* (including *Monotreus* and *Chelonodon* of authors), and *Arothron* in this group, and restricted them to his family Tetraodontidea. Two common features among all of these genera are an extremely broad, stout head (related to a neurocranium with heavy broad frontal bones), and prominent lateral ethmoids separated principally by a short, stout mesethmoid. This is essentally the condition found in *Ephippion,* but the mesethmoid is slightly more narrow and elongate than in its closest ally, *Tetraodon.* According to Fraser-Brunner (1943:12), the sphenotics form a narrow projection in *Ephippion,* but a broader, flattened lobe in *Tetraodon. Arothron,* an Indo-Pacific genus which differs in a number of cranial characters and structure of the nasal organ, is not treated here, as it is obviously more distantly related to *Ephippion* than is *Tetraodon.* The nasal organs of *Ephippion* and *Tetraodon* are quite similar; these appear as open pits surrounded by elaborate fleshy tentacles (Fig. 1).

Regan (1902:292) and Fraser-Brunner (1943:14) have pointed out that such a nasal organ is a derived character resulting from a fusion of the ancestral double nasal opening, and the fleshy tentacles are the resultant vestige of the nasal papilla. *Ephippion* has two large lateral tentacles,

and a third smaller flap which borders the posterior margin of the nasal opening. *Tetraodon* differs in lacking a discrete third tentacle or flap on the posterior nostril margin.

The most distinctive and diagnostic feature of *Ephippion* is the carapace of bony plates which enclose much of the anterior portions of the trunk. No other tetraodontoid possesses such modifications. The structure must be considered a derived character, and cannot be considered as homologous to the similar structures found in the Ostraciontidae. To do so would imply that all other specialized adaptations common to all tetraodontoids were acquired by an ancestral stock which possessed a carapace, and that this structure was then independently lost by all forms except *Ephippion.* Furthermore, such a view would imply a much closer relationship between tetraodontids and ostraciontids than has previously been accepted. Certainly a more logical hypothesis would be to consider the carapace of *Ehippion* as a specialized modification of the prickles. Analagous modifications of prickles can be found in various groups of Diodontidae, and in the tetraodontoid genus *Xenopterus.* It appears, therefore, that *Ephippion* is an estuarine-marine offshoot from an ancestral *Tetraodon* stock. This ancestor probably inhabited the fresh waters of Africa, the present range of *Tetraodon* (sensu stricto).

Table 1.— General distribution of Atlantic species of Tetraodontidae by major geographic regions.

	Western North Atlantic (Canada to Florida)	Gulf of Mexico	Caribbean	Western South Atlantic	Europe, Atlantic Coast	Africa, Atlantic Coast	Circumglobal
Lagocephalus							
lagocephalus	x		x		x	x	x
laevigatus	x	x	x	x		x	
Sphoeroides							
pachygaster	x	x	x	x		x	x
dorsalis	x	x	x				
marmoratus						x	
yergeri			x				
tyleri			x	x			
spengleri	x	x	x	x			
greeleyi			x	x			
testudineus	x	x	x	x			
maculatus	x						
nephelus	x	x	x				
georgemilleri			x				
parvus		x					
Colomesus							
psittacus			x	x			
*asellus**			x	x			
Ephippion							
guttifer					x	x	
TOTAL	8	7	13	8	2	5	2

*Fresh water, northern and central South America.

Table 2.— Pectoral fin ray counts (both fins) of Atlantic species of Tetraodontidae.

	Number of Rays							
	13	14	15	16	17	18	19	20
Lagocephalus								
lagocephalus	6	15	8	9				
laevigatus			2	6	44	27	1	
Sphoeroides								
pachygaster		32	18	25	5			
dorsalis			38	60	7			
marmoratus	1	16	5					
yergeri	7	47	4					
tyleri		1	43	26				
spengleri	97	32						
greeleyi	2	58	57	1				
testudineus	5	89	257	43				
maculatus			83	144	4			
nephelus	36	294	56					
georgemilleri			3	14	1			
parvus	4	82	106	9				
Colomesus								
psittacus					16	72	17	
asellus	5	41	74	17				
Ephippion								
guttifer						5	36	5

Table 3.— Anal fin ray counts of Atlantic species of Tetraodontidae.

	Number of Rays								
	6	7	8	9	10	11	12	13	14
Lagocephalus									
lagocephalus						2	14	2	
laevigatus						1	22	16	2
Sphoeroides									
pachygaster		2	18	19					
dorsalis		47							
marmoratus	1	10							
yergeri	3	27							
tyleri	3	29							
spengleri	6	40	1						
greeleyi	1	46							
testudineus	6	145	1						
maculatus		23							
nephelus	4	57							
georgemilleri		9							
parvus	5	61	1						
Colomesus									
psittacus				4	23	23			
asellus			1	13	33	24			
Ephippion									
guttifer			4	17	2				

Table 4.— Dorsal fin ray counts of Atlantic species of Tetraodontidae.

	Number of Rays								
	7	8	9	10	11	12	13	14	15
Lagocephalus									
lagocephalus							1	14	5
laevigatus						1	15	17	6
Sphoeroides									
pachygaster		6	34	1					
dosalis		49							
marmoratus		10	1						
yergeri	2	28							
tyleri	1	34							
spengleri	7	43							
greeleyi	3	46							
testudineus	5	150	3						
maculatus	1	36							
nephelus	3	86	5						
georgemilleri		8	1						
parvus		64	8						
Colomesus									
psittacus				9	43	1			
asellus				19	50	3			
Ephippion									
guttifer			1	17	5				

Table 5.— Measurements of *Lagocephalus lagocephalus* (14 subadults and adults) and *L. laevigatus* (20).

	Range (% SL)		Mean (% SL)		Standard Deviation	
	lagocephalus	*laevigatus*	*lagocephalus*	*laevigatus*	*lagocephalus*	*laevigatus*
Standard length (mm)	114-510	99-350	272.6	225.6	—	—
Head length	27.2-35.0	28.5-35.2	30.9	31.6	1.91	1.83
Snout length	12.4-15.6	14.1-18.8	13.9	16.6	0.90	1.14
Least bony interorbital width	8.9-13.9	11.1-13.8	10.1	12.2	1.24	0.77
Eye diameter	4.1-7.6	6.4-10.6	5.6	8.0	0.97	1.19
Pectoral fin length	14.4-19.1	13.6-18.6	16.6	15.5	1.60	1.39
Depressed dorsal fin length	13.6-18.0	16.2-19.8	15.9	17.9	1.31	1.21
Depressed anal fin length	14.1-18.5	14.9-19.8	16.3	17.5	1.31	1.22
Caudal fin length	10.7-14.7	10.9-15.6	13.0	12.6	1.21	1.48

Table 6.— Measurements of *Sphoeroides pachygaster* (20 subadults and adults), *S. dorsalis* (20), and *S. marmoratus* (9 adults).

	Range (% SL)			Mean (% SL)			Standard Deviation		
	pachy-gaster	*dorsalis*	*mar-moratus*	*pachy-gaster*	*dorsalis*	*mar-moratus*	*pachy-gaster*	*dorsalis*	*mar-moratus*
Standard length (mm)	90-188	64-148	89-141	131.7	97.2	107.8	—	—	—
Head length	36.0-45.5	32.3-40.0	33.5-38.7	40.3	36.8	35.7	1.97	1.79	1.57
Snout length	17.1-22.0	18.9-24.5	17.6-20.2	19.1	21.6	19.2	1.25	1.06	0.79
Least bony interorbital width	6.2-12.2	2.7-3.9	3.7-5.0	8.7	3.5	4.1	1.60	0.30	0.49
Eye diameter	8.1-13.4	6.1-10.0	6.0-8.6	10.0	8.1	7.8	1.60	0.90	0.83
Pectoral fin length	13.1-16.4	12.8-16.9	12.0-15.0	14.7	14.7	13.3	0.94	0.96	0.87
Depressed dorsal fin length	11.5-14.7	14.9-18.3	14.0-16.9	13.0	16.7	15.5	0.93	0.96	0.96
Depressed anal fin length	10.5-14.5	12.1-16.1	14.0-16.5	12.8	14.1	15.5	1.00	0.98	0.83
Caudal fin length	12.8-16.3	16.1-20.9	19.1-22.3	14.5	18.7	20.9	1.12	1.49	1.10

Table 7.— Measurements of *Sphoeroides yergeri* (20 adults), *S. tyleri* (15), and *S. spengleri* (20).

	Range (% SL)			Mean (% SL)			Standard Deviation		
	yergeri	*tyleri*	*spengleri*	*yergeri*	*tyleri*	*spengleri*	*yergeri*	*tyleri*	*spengleri*
Standard length (mm)	57-79	62-96	72-133	60.8	82.9	91.7	—	—	—
Head length	34.0-38.2	35.2-39.0	33.4-38.6	35.6	37.1	35.9	1.07	0.96	1.20
Snout length	15.9-20.7	18.5-21.4	17.4-22.2	18.1	20.1	19.4	1.23	1.03	1.24
Least bony interorbital width	2.7-3.6	3.2-4.8	4.4-6.1	3.2	4.0	5.3	0.27	0.47	0.47
Eye diameter	6.8-9.7	7.0-11.1	4.7-8.8	8.2	9.0	7.2	0.78	0.91	1.07
Pectoral fin length	12.1-14.9	14.8-17.7	10.4-14.3	13.7	16.4	12.3	0.70	0.82	0.84
Depressed dorsal fin length	14.6-18.0	16.6-20.7	13.2-17.2	16.0	17.7	15.4	0.89	1.12	1.17
Depressed anal fin length	11.7-14.5	13.1-17.6	14.0-17.4	13.2	14.6	15.4	0.86	1.10	1.04
Caudal fin length	21.3-26.1	19.6-24.6	17.3-21.8	23.1	22.0	18.9	1.27	1.44	1.07

Table 8.— Measurements of *Sphoeroides greeleyi* (20 adults), *S. testudineus* (20), and *S. maculatus* (20).

	Range (% SL)			Mean (% SL)			Standard Deviation		
	greeleyi	*testudineus*	*maculatus*	*greeleyi*	*testudineus*	*maculatus*	*greeleyi*	*testudineus*	*maculatus*
Standard length (mm)	74-139	91-160	83-217	100.5	118.5	120.4	—	—	—
Head length	34.3-38.0	32.5-38.1	36.5-41.0	35.9	35.3	38.3	1.05	1.26	1.33
Snout length	17.5-21.3	16.1-19.0	18.5-22.7	20.1	17.8	20.0	0.85	0.94	1.05
Least bony interorbital width	4.0-7.3	6.0-8.3	5.0-7.0	5.4	7.3	5.8	0.85	0.57	0.64
Eye diameter	5.0-8.0	5.4-9.7	4.6-9.7	6.6	7.5	7.9	0.90	1.04	1.58
Pectoral fin length	13.1-17.8	12.9-16.7	13.8-18.4	15.1	14.9	15.8	1.14	0.83	1.05
Depressed dorsal fin length	16.0-25.2	17.1-21.5	14.6-18.5	18.9	19.0	16.9	2.06	1.13	0.94
Depressed anal fin length	14.3-18.9	14.7-18.6	12.4-16.7	16.5	16.6	15.8	1.23	1.22	1.09
Caudal fin length	19.7-26.2	20.0-25.7	15.4-22.9	23.8	24.1	20.2	1.60	1.51	1.78

Table 9.— Measurements of *Sphoeroides nephelus* (20 adults) *S. georgemilleri* (9 subadults and adults), and *S. parvus* (20 adults).

	Range (% SL)			Mean (% SL)			Standard Deviation		
	nephelus	*george-milleri*	*parvus*	*nephelus*	*george-milleri*	*parvus*	*nephelus*	*george-milleri*	*parvus*
Standard length (mm)	102-215	53-95	51-97	153.2	76.0	72.8	—	—	—
Head length	33.6-39.2	34.0-38.2	33.4-38.5	36.7	35.8	35.9	1.42	1.61	1.30
Snout length	18.0-25.2	18.7-22.2	16.6-19.4	21.6	20.2	17.6	1.64	0.97	0.80
Least bony interorbital width	3.2-5.1	6.4-8.1	4.4-6.4	3.9	7.4	5.2	0.47	0.60	0.48
Eye diameter	4.9-8.8	7.2-8.8	6.1-11.0	6.7	7.9	8.4	0.96	0.63	1.29
Pectoral fin length	13.2-17.7	14.4-17.4	15.4-21.0	15.5	15.9	17.7	1.27	1.04	1.56
Depressed dorsal fin length	14.5-19.4	18.7-21.0	16.0-20.0	17.1	19.8	18.3	1.41	0.83	1.09
Depressed anal fin length	12.1-15.8	14.8-18.8	13.7-17.7	14.3	17.1	15.4	1.06	1.04	1.25
Caudal fin length	16.3-21.8	22.2-29.8	19.1-23.4	19.5	24.8	20.9	1.73	2.44	1.35

Table 10.— Measurements of *Colomesus asellus* (13 subadults and adults) and *Colomesus psittacus* (11).

	Range (% SL)		Mean (% SL)		Standard Deviation	
	psittacus	*asellus*	*psittacus*	*asellus*	*psittacus*	*asellus*
Standard length (mm)	101-268	22-85	167.7	54.1	—	—
Head length	36.5-41.0	34.3-40.0	37.8	36.6	1.23	1.84
Snout length	14.1-17.7	12.3-14.8	15.8	13.7	1.21	0.91
Least bony interorbital width	12.1-16.7	9.0-19.1	14.8	14.4	1.48	3.50
Eye diameter	3.4-5.9	7.1-10.9	4.6	8.9	0.79	1.23
Pectoral fin length	11.6-14.9	13.6-16.2	13.5	15.2	0.92	0.85
Depressed dorsal fin length	15.8-21.3	17.4-24.5	18.4	21.7	1.76	2.44
Depressed anal fin length	15.8-21.3	17.4-24.5	18.8	21.2	1.62	2.18
Caudal fin length	20.0-27.6	21.8-29.1	23.3	23.9	2.09	2.44

Table 11.— Measurements of *Ephippion guttifer* (18 subadults and adults).

	Range % SL	Mean % SL	Standard Deviation
Standard length (mm)	106-402	172.7	—
Head length	29.9-37.8	34.8	2.14
Snout length (mm)	14.5-18.2	16.1	0.97
Least bony interorbital width	12.3-16.6	14.4	1.09
Eye diameter	5.1-9.0	7.4	1.13
Pectoral fin length	14.4-19.1	16.5	1.31
Depressed dorsal fin length	21.1-25.2	22.9	1.45
Depresed anal fin length	17.5-24.6	22.0	1.97
Caudal fin length	19.7-33.2	27.9	3.58

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